
Wisconsin Karner Blue Butterfly Habitat Conservation Plan and Environmental Impact Statement

Appendix A. Karner Blue Butterfly Biology

The following summary of Karner blue butterfly biology and ecology is excerpted from the USFWS's working draft Karner Blue Butterfly Recovery Plan (USFWS 1997). *Text is reproduced here without editing; only formatting was changed.* For a complete copy of the federal Recovery Plan, please contact the Green Bay Field Office of the USFWS.

Since this appendix consists of material excerpted from another document, some clarification is merited. The federal Recovery Plan was used as the source for this appendix because it includes the most succinct and current summary of Karner blue butterfly biology. References to "this recovery plan" found in this excerpt refer to the working draft Karner Blue Butterfly Recovery Plan (USFWS 1997), *not* the Wisconsin Karner Blue Butterfly HCP and EIS documents (the HCP is not a federal recovery plan). Similarly, mention of appendices made in this excerpt refers to appendices of the working draft Karner Blue Butterfly Recovery Plan, not material appended to the HCP and EIS. To reduce redundancy and costs, references cited in the excerpt are not included in Chapter VIII of the EIS. Readers should refer to the recovery plan for proper citations. However, table and figure references included here do refer to tables and figures in the excerpt.

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Part I. Introduction

Karner blue butterfly (*Lycaeides melissa samuelis* Nabokov) differs from many other federally listed species, particularly other arthropods, in that it is geographically widespread. In some areas it has been or continues to be locally abundant. Much of its original savanna/barrens habitat has been destroyed by development or degraded by succession, and has not been replaced by other suitable habitat, especially in the eastern part of its range and its geographic range margins. Fragmentation of the landscape from larger suitable habitats, to smaller sometimes isolated habitats, is also suspected of contributing to the problem. The loss of suitable habitat resulted in a rapid decline in population numbers and extirpation of large populations across its range, and prompted its listing as a federally endangered species.

Karner blue butterfly ecology is closely interwoven with its habitat. These habitats provide food resources and key microhabitats for the butterfly. The larval stage is known to feed only on one species of plant, wild lupine (*Lupinus perennis*). Adults require nectar sources to survive and lay sufficient eggs. Several life stages of the butterfly benefit from the variety of microhabitats often provided in some types of barrens, savanna, silvicultural, and rights-of-way ecosystems. These favorable microhabitats will disappear in a few to many years from normal successional processes, so Karner blue persistence is dependent on disturbance to renew existing habitat or to create new habitats. The distribution and dynamics of these ephemeral habitats form the ecological basis for recovery planning.

Taxonomy and Description

Karner blue butterfly was proposed for federal listing on January 21, 1992 (57 FR 2241), and on December 14, 1992 it was listed as federally endangered rangewide (57 FR 59236). The taxonomy follows Lane and Weller (1994) who have conducted the most recent review of the taxonomy of Karner blue butterfly. Karner blue is a member of the genus *Lycaeides* (Lepidoptera: Lycaenidae: Polyommatainae) (Elliot 1973, Nabokov 1943, 1949). In North America there are two species of *Lycaeides*, *L. idas* (formerly *L. argyrognomon*) and *L. melissa* (Higgins 1985, Lane and Weller 1994). *Lycaeides melissa* is comprised of six subspecies, *L. m. melissa*, *L. m. annetta*, *L. m. inyoensis*, *L. m. mexicana*, *L. m. pseudosamuelis*, and *L. m. samuelis* (Lane and Weller 1994). The taxonomy for this group was conducted by Vladimir Nabokov in the 1940's. Sometime after this work was published, Nabokov commented in private letters that Karner blue should be classified as a distinct species (Nabokov 1952, 1975, 1989). Nabokov noted that the male genitalia of *L. m. melissa* were very variable geographically, but the male genitalia of *L. m. samuelis* were remarkably constant over the entire range of the subspecies. Moreover, *L. m. samuelis* uses only one host plant throughout its geographic range, while *L. m. melissa* uses many species of host plant.

The taxonomic work to elevate *L. m. samuelis* to the species level was never completed, and the

currently accepted status of Karner blue butterfly is subspecific (Miller and Brown 1983, Nabokov 1943, 1949, Opler 1992, Opler and Krizek 1984).

Packer (1994) surveyed electrophoretic variation at 34 loci among Wisconsin (n=17) and New York (n=13) Karner blue butterflies and a Minnesota (n=15) population of melissa blue. An average of 16.2-20.1 haploid genomes were sampled for each locus, and only 16 of the loci exhibited any electrophoretic variation among samples. Nei's genetic identity values were high (>0.967), and Packer concluded that the electrophoretic evidence does not provide evidence that Karner blue is a separate species from melissa blue. Electrophoretic data, however, are not usually reliable for separating closely related species, and this electrophoretic analysis cannot be used to determine the taxonomic status of Karner blue, because no relevant outgroup is identified for comparison.

The forewing length of adult Karner blue butterflies is 1.2-1.4 cm for males and 1.4-1.6 cm for females (Opler and Krizek 1984). The wing shape is rounded and less pointed than *L. m. melissa*, especially in the female hind wing (Nabokov 1949). The upper (dorsal) side of the male wing is a violet blue with a black margin and white fringed edge. The female upper side ranges from dull violet to bright purplish blue near the body and central portions of the wings, and the remainder of the wing is a light or dark gray-brown, with marginal orange crescents typically restricted to the hind wing. Both sexes are a grayish fawn color on the ventral side. Near the margins of the underside of both wings are orange crescents and metallic spots. The black terminal line along the margin of the hind wing is usually continuous (Klots 1979, Nabokov 1944). Male genitalia is the most reliable character for distinguishing adult *L. m. samuelis* from other subspecies (and species) (Nabokov 1944, 1949).

The eggs of Karner blue are tiny and radially symmetric with an approximately 0.7 mm diameter, somewhat flattened, and pale greenish-white in color (Dirig 1994 provides a photograph). The surface is deeply reticulated with a fine geometric pattern (Spoor 1994 provides some scanning electron micrographs of the reticulation). Larvae are a pea-green color, pubescent and dorsally flattened, with a brown-black to black head capsule. The head is often not visible as it is tucked under the body. Older larvae have pale green (to white) lateral stripes, and a dark green longitudinal stripe dorsally. In pre-pupal larvae the lateral stripes become less distinct and the color becomes a duller green. Larvae have four instars (Savignano 1990), and have three glandular structures that are known to mediate interactions with ants in other species of Lycaenidae (Savignano 1994 and references therein). Some of these glandular structures mediate interactions with ants in Karner blue, but it is not known what is secreted by any of the structures, and it is not known if any of the structures are active throughout larval life. Pupae are bright green and smooth, changing to a light tan with hints of purple shortly before emergence when the pharate adult cuticle separates from the cuticle of the pupal case.

Distinguishing Karner Blue from Similar Species. In eastern U.S., Karner blue butterfly can be confused readily with eastern-tailed blue (*Everes comyntas*) and less readily with spring azure (*Celastrina argiolus* complex) (Opler 1992, Scott 1986). Eastern-tailed blues are on average

smaller than Karner blue and they have black projections or "tails" on the outer angle of the hind wings (Opler 1992, Scott 1986). These tails may be broken off, but usually leave some remnant indicating their former presence. On the underside of the wings, orange crescents are absent on the forewing, and four spots, two large and two small, are present on the hind wing (Opler 1992, Scott 1986). It may be difficult to distinguish a large male eastern-tailed blue from a small male Karner blue when they are in flight. Spring azures lack the orange crescents on the under sides of their wings (Opler 1992).

In the midwest, Karner blue butterflies can be confused with Nabokov's blue (*L. idas nabokovi*), melissa blue (*L. melissa melissa*), eastern- and western-tailed blue (*Everes comyntas* and *E. amyntula*), Reakirt's blue (*Hemiargus isola*), greenish blue (*Plebius saepiolus*), marine blue (*Leptotes marina*), acmon blue (*Icaricia acmon*), spring azure (*Celastrina argiolus* complex), and silvery blue (*Glaucopsyche lygdamus*) (Opler 1992, Scott 1986). Species occurrence varies throughout the midwest and to determine the species present locally, consult local guides and checklists. Eastern-tailed blue is the only species that is confused readily with Karner blue. Spring azure, silvery blue, Reakirt's blue, and marine blue, lack the orange crescents on the under sides of their wings (Opler 1992, Opler and Krizek 1984, Scott 1986). Eastern- and western-tailed blues have tails (as described above), orange crescents are absent on the underside of the forewing, and there are, respectively, four or one orange spot(s) on the hind wing (fewer than Karner blue). Greenish blue has one or more orange marginal crescents, which are, however, much smaller in size than the spots on Karner blue. The marginal crescents on the dorsal side of the male acmon blue hind wing, tend to be more pink than orange (Opler 1992). Melissa blue can be distinguished from Karner blue by having orange banding on the upper (dorsal) side of the forewing, genitalic differences and differential habitat use (Nabokov 1943, 1949, Scott 1986). Melissa blue larvae can feed on *Astragalus* sp., *Glycyrriza lepidota*, *Lupinus* sp., and several other species (Scott 1986). The occurrence of melissa blue comes closest (30 miles) to Karner blue sites in southeastern Minnesota. The range of Nabokov's blue, *L. idas nabokovi*, overlaps with Karner blue in certain areas, but Karner blue is typically found in oak and pine savanna/barrens, whereas Nabokov's blue is found primarily in forest clearings (Masters 1972). Also, the two species have different host plants. Karner blue feeds exclusively on wild lupine (*Lupinus perennis*), and Nabokov's blue feeds on dwarf bilberry (*Vaccinium cespitosum*) (Nielsen and Ferge 1982). Although there are superficial differences in coloration between these two subspecies (Masters 1972), unequivocal identification would require dissection and examination of the male genitalia (Nabokov 1944). Interested readers should consult the cited references for more details.

Distribution

Historically the Karner blue butterfly occurred in a geographic band between 41° and 46° N latitude extending from Minnesota to Maine (Dirig 1994). The butterfly is commonly found on sandy soil types that have populations of *Lupinus perennis* (the only known larval food source), and often inhabits communities similar to oak and pine savanna/barrens communities. In this recovery plan, the term "lupine" will refer to *L. perennis* to the exclusion of all other species of *Lupinus*.

Dirig (1994) reviewed all of the locality records of Karner blue he could find, whether or not they were confirmed with vouchered specimens. His work is an exhaustive summary of the reports of Karner blue occurrence. To establish a definitive historic geographic range, the Recovery Team included only locality records with confirmed specimens. The Recovery Team contacted Dr. Robert Dirig for further information on some of his records, which he promptly provided. Information from him was especially critical for evaluating records from Pennsylvania, New Jersey, Maine, and Wisconsin. A summary of some of these findings are shown in Figures 8-11 below.

The historic northern limit of the butterfly corresponds roughly with the northern limit of lupine (Dirig 1994), but the current distribution indicates that the butterfly has contracted away from this limit. Many of the most northern populations of Karner blue have been extirpated, such as at Norway, ME, Webster, NH, Watertown, NY, throughout Ontario, Canada, Wausaukee, WI (this record is being checked), and Anoka, MN. Lupine has been reported from as far north as northern Vermont, and Elk Rapids, MI, but there are no records of Karner blue from these sites. The only populations of Karner blue now near the northern limit of lupine occur within the Superior Outwash Recovery Unit in Wisconsin.

The historic western limit of the butterfly roughly corresponds with the western limit of lupine (Dirig 1994), and butterfly distribution appears to have contracted away from this limit as well. Although lupine occurs as far west as central Minnesota, the western-most record of Karner blue is at Anoka, MN, approximately 50 miles to the east. The Anoka population was extirpated sometime after 1984. The Iowa populations on the southwest fringe are also extirpated. Currently, the western-most populations of Karner blue occur in the Superior Outwash Recovery Unit and a small population occurs at the Whitewater Wildlife Management Area in southeast Minnesota in the Paleozoic Plateau Recovery Unit. The historic eastern limit of the butterfly roughly corresponds with the eastern limit of lupine. No historic or current records of Karner blue exist in Connecticut, Rhode Island, eastern Massachusetts, or eastern Long Island, but these native habitats were converted to incompatible human uses long ago, so the previous presence of the butterfly cannot be verified. Nonetheless, based on the biology of the butterfly and information on the native habitats, the butterfly probably inhabited these areas in the past. The eastern-most historic

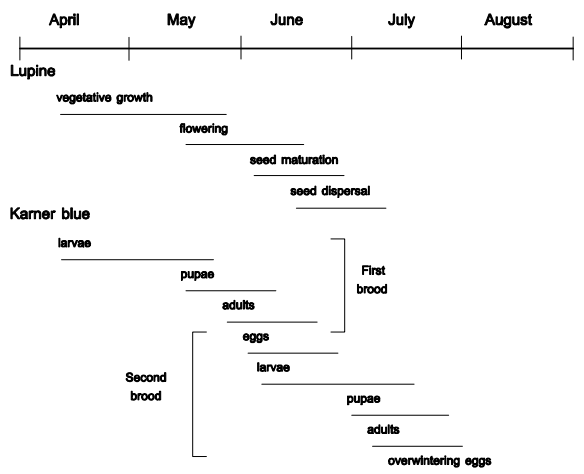
records of Karner blue exist from southwest Maine and throughout the Merrimack River valley

system in New Hampshire and Massachusetts, but currently, this eastern-most population has contracted to a very small population near Concord, NH.

Unlike the other geographic limits, the historic southern limit of the butterfly does not correspond to the southern distribution of lupine. The distribution of lupine extends farther south than Karner blue in eastern U.S. along the eastern Appalachian Mountains and the Atlantic Coastal Plain, and in central U.S. in Illinois (Dirig 1994). Some of the historic records of Karner blue along this southern limit are uncertain. The southern-most record near Coyington, IN, is probably erroneous. The recovery team could not find a specimen associated with this record, and lupine has not been recorded from near this locality. The records from several Pennsylvania localities could not be confirmed. These localities are recorded by Dirig (1994) and were reported to him by Dr. A. Shapiro. The recovery team corresponded with Dr. Shapiro, who stated that he could not locate a specimen corresponding with any of his reported Pennsylvania localities. The only confirmed record in Pennsylvania is from Wayne County. Several of the NY records along the Delaware River and the eastern branch of the Susquehanna River were confirmed with specimens. The New Jersey record may be erroneous, although specimens exist. Schweitzer (personal communication) suggested that the specimens were unlikely to have been collected from New Jersey and may have been mis-labelled NY specimens. The record from Brooklyn, NY, has been confirmed. The lack of correspondence of the southern limits of Karner blue and lupine has not been adequately addressed. Dirig (1994) suggested that the southern limit of Karner blue may follow the band of 80-100 days continuous winter snow cover, which he hypothesized was necessary for high overwintering egg survival. Many other hypotheses could explain the southern distribution limit of Karner blue.

Despite this uncertainty, similar to the other geographic limits, the distribution of Karner blue has contracted away from its historic southern limit. Populations have been extirpated from southern New York, Pennsylvania, Ohio, Illinois, and Iowa. In Indiana, the distribution has contracted. Once present throughout northern Indiana, it now occurs only in a few localities in northwestern Indiana, associated with the dunefields and dune and swale complexes near the southern end of Lake Michigan.

Figure 1. Phenology of Karner blue and lupine. In colder (warmer) areas and years phenologies will be delayed (advanced).



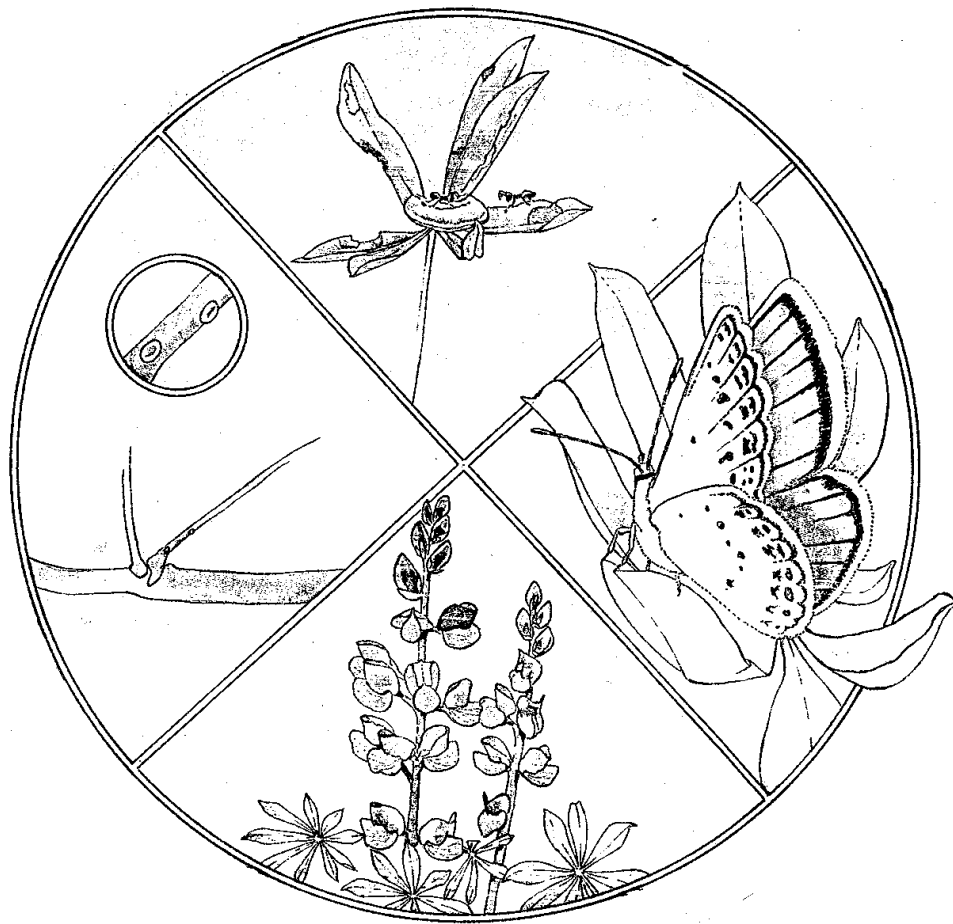
As of fall, 1996, populations of Karner blue existed in Indiana, Michigan, Minnesota, New Hampshire, New York and Wisconsin. Almost all known extant populations occur on sandy soils associated with glacial outwash plains and terraces, glacial moraines, the shores and bottoms of glacial lakes, the glacial shores of existing lakes, and dissected sandstone outwashes (Andow et al. 1994 and references therein, Appendix B). Wisconsin and Michigan have the largest number of local populations with the greatest numbers of individuals, and New York also has one large population (Baker 1994). Many local populations of the butterfly appear extirpated, and the states of Iowa, Illinois, Ohio, Pennsylvania, Massachusetts, Maine, and the Canadian

province of Ontario no longer support populations of the butterfly (Baker 1994). More detailed descriptions of the historic and current distribution of Karner blue are provided in Appendix B.

Life History and Ecology

Karner Blue Butterfly. The life history of Karner blue butterfly has been studied by Scudder (1869), Dirig (1976, 1994), Cryan and Dirig (1978), Savignano (1990) and Lane and Welch (1994). Karner blue butterfly is bivoltine, which means that it completes two generations per year (Figure 1). In typical years, first brood larvae hatch from overwintered eggs in mid- to late April and begin feeding on wild lupine (*Lupinus perennis*), the only known larval food source (Figure 2). Larvae pass through four instars, between which the relatively soft larval exoskeleton is shed. Feeding by first and second instar larvae results in tiny, circular holes in the lupine leaves while older larvae eat all but the upper or lower epidermis, creating a characteristic window-pane appearance (see Swengel 1993b for detailed description). Larvae feed for approximately 3-4 weeks and pupate in late May to early June. Larvae are commonly tended by ants. Mature larvae enter a wandering phase, after which the pre-pupal larvae attach themselves to various substrates with a silk thread. Known pupation sites include in the leaf litter, on stems and twigs, and occasionally on lupine leaves (Dirig 1976, Dirig and Cryan 1978, Savignano, personal communication). Dirig (1976) reported that pupation generally lasted seven to eleven days in the field. Laboratory-reared pupae took eight or nine to eleven days before eclosing (Savignano 1990, Lane, personal communication). Adults begin emerging in late May through mid-June. Peak flight for males usually precedes peak flight for females

Figure 2. Illustration of life history stages of karner blue butterfly, showing (top) larva on a lupine leaflet tended by ants, (left) eggs laid on a lupine leaf petiole, (right) adult on a lupine leaf, and (bottom) flowing lupine inflorescence.



by a couple of days. Adults are believed to live an average of 4-5 days but can live as long as 2-3 weeks. First flight adult females lay their eggs primarily on lupine plants, often singly on leaves, petioles, or stems, or occasionally on other plants or duff close to lupine plants.

Second brood eggs hatch in 5-10 days, depending on the ambient temperature. Second generation larvae can be found feeding on wild lupine leaves and flowers from early June through late July. Typically, one larvae can survive on one large lupine stem, however, it moves from leaf to leaf on the lupine stem, often returning to leaves fed on during earlier instars, and it may even move to other lupine stems (Lane, personal communication). Larvae are found often on the lower parts of the stems and petioles. Second brood larvae are also typically tended by ants, but during midday on hot days tending may be reduced. Pupae are also frequently tended by ants (Lane, personal observation).

Second brood adults begin to appear in early to mid-July and fly until mid-August. Flight phenology may be delayed because of cool wet summers and result in an adult flight period lasting through late August (Bleser 1992, Lane 1996). The peak flight period usually lasts one to two weeks. Generally, there are about 3-4 times as many adults in the second brood compared with the first brood (Schweitzer 1994a), but exceptionally poor years can occur where the second brood is no larger than the first brood. First brood may typically be smaller because of high overwintering mortality of eggs, the inability of larvae to find lupine in the spring, or greater oviposition success of first flight females. Maxwell and Givnish (1993) surveyed Karner blue populations at 46 locations at Ft. McCoy, Wisconsin during 1993, and found that locations with high first flight butterfly counts also had high second flight counts ($r^2 = 0.674$), and that populations were 3-4 times as abundant during the second flight. Second flight females usually land on green (non-senesced) lupine, crawl down the stem, and lay eggs primarily on grasses and sedges, other plant species, leaf litter near lupine stems, and occasionally on lupine (Lane 1995). In general, insects that overwinter in the egg stage often lay their eggs on various materials close to the ground because these sites afford better winter protection (Bernays and Chapman 1994). The eggs laid by second flight females are the overwintering stage (evidence summarized by Haack 1993) and studies by Spoor (1994) and Van Luven (1993, 1994a) provide strong experimental evidence of this. Spoor (1994) observed second brood eggs through November and determined hatching rates of these eggs the following spring. Researchers in New Hampshire and Wisconsin have successfully overwintered eggs for rearing experiments (VanLuven 1993, 1994a; Meehl, personal communication).

Karner blue adults are diurnal and initiate flight between 8:00-9:00 a.m. and continue until about 7:00 p.m., a longer flight period than most butterflies. Adult activity decreases in very hot weather, at temperatures lower than 75° F, during heavy to moderate rains, or during extremely windy conditions.

Lupine Food Resource. *Lupinus perennis* is a member of the pea family (Fabaceae) and has the common names wild lupine and blue lupine. Lupine is the only known food plant for larval

Karner blue and is an essential component of its habitat. Two varieties have been identified: *Lupinus perennis* var. *occidentalis* S. Wats. and *L. perennis* var. *perennis* L. (Ownbey and Morley 1991). The varieties are morphologically similar except the former has spreading pilose hairs and the latter thinly pubescent hairs (Boyonoski 1992). Although Karner blue may use both varieties, the relation between Karner blue and these lupine varieties is not known. The inflorescence is a raceme of numerous small flowers which are two lipped, with the upper lip two-toothed and the lower lip unlobed. Flower color ranges from blue to violet and occasionally white or pink (Gleason and Cronquist 1993). Peak bloom typically occurs from mid-May to late June within the geographic range of Karner blue, but varies depending upon weather, degree of shading, and geographic location in its range. Stem density and flowering is greatest in open- to partial-canopied areas, although areas receiving high solar radiation can have low lupine densities and may be less than ideal habitat (Boyonoski 1992). Plants in dense shade rarely flower.

Lupine distribution extends from Minnesota east to New England, extending southward along the eastern Appalachian Mountains to southern Virginia and along the eastern coastal plain to Georgia wrapping around the Gulf coastal plain to Louisiana (Dirig 1994). Surveys of lupine throughout its northern range all report populations to be declining and many sites have been extirpated (Boyonoski 1992, Cuthrell 1990, Grigore 1992). The primary cause of this decline appears to be loss of habitat from conversion to housing, retail, light industrial, and agricultural development, and degradation of habitat because of the deep shade that develops when disturbance is interrupted.

Lupine abundance and Karner blue. Management for sufficient lupine is critically important for Karner blue, because it is the only food plant for the larvae. Significant increases in the abundance of lupine will usually not be detrimental to Karner blue, and may in many cases be beneficial. Lupine, however, is not the only factor limiting Karner blue butterfly subpopulations, so it is important to manage for additional factors that are important for Karner blue in addition to lupine.

A positive association between lupine abundance and Karner blue abundance or persistence would indicate that lupine could be a factor limiting Karner blue populations. Several researchers have found such a positive correlation between lupine abundance and number of Karner blue butterfly adults in NY, MI, and WI (Herms 1996, Maxwell and Givnish 1993, Papp 1993, Savignano 1994b). Savignano (1994b) found a significant correlation between Karner blue numbers and the number of lupine rosettes in New York studies. One site had abundant lupine but few butterflies, and Savignano (1994b) suggested that a dearth of nectar plants limited the butterfly.

Lupine was not a good predictor of Karner blue abundance in Michigan and Minnesota studies. Lawrence (1994) noted that the vast majority of lupine plants did not support Karner blue larvae

at the Allegan State Game Area in Michigan. Herms (1996 [same data as Papp 1993]), however, surveyed seven sites and found a significant positive relationship between lupine and Karner blue abundance at the Allegan State Game Area. Lawrence's study included more sites than Herms', and Herms' result appears to be strongly affected by a few sites, so Lawrence's remains the more scientifically credible result. The site with the densest lupine populations did not support Karner blue butterflies in Minnesota, however this site is over 2.5 km from occupied habitat (Lane 1994a). Lawrence (1994) and Lane (1994a) suggested that other factors, such as microhabitat may influence Karner blue butterfly population dynamics.

Lupine abundance at a site may vary temporally within a year or between years. Late emergence or early senescence of lupine might result in larval starvation. The timing of lupine senescence varies with canopy cover and annual weather. Maxwell and Givnish (1996) found that with increased shrub cover, the onset of lupine senescence was later and less abrupt. Lane (1994b) observed that second brood larvae disappeared from lupine that senesced early. These individuals probably died because lupine density was low and successful dispersal to another plant was improbable.

It is unlikely that a single factor, such as the density of lupine, would account for variation in abundance of Karner blue throughout its range. In places where it does, however, such as in the Glacial Lake Albany Recovery Unit in New York and Ft. McCoy, WI, it suggests that Karner blue populations might be enhanced by increasing the amount of lupine available. In those localities where there is a poor correlation between lupine abundance and adult Karner blues, such as in the Allegan State Game Area and the Paleozoic Plateau Recovery Unit, other factors may be important.

Lupine quality and Karner blue. Lupine quality may influence Karner blue butterfly ecology. Within species variation in plant quality has been shown to be related to variation in plant chemistry, morphology, health, etc. (Bernays and Chapman 1994). Chemical factors most likely to influence food quality are nutrient composition and secondary plant compounds. The concentrations of proteins and sugars have been shown to vary with leaf position on the plant, leaf age, and sun received for several species (Bernays and Chapman 1994). *Lupinus* species have secondary plant compounds, typically alkaloids, that have been shown to influence their suitability for insect food. Levels of alkaloids in lupine vary with plant part and are highest in reproductive parts and the epidermis (Bernays and Chapman 1994). The fact that Karner blue larvae feed solely on lupine is strong evidence that they are adapted to the alkaloids in lupine, but the role of these factors in the ecology of Karner blue is unknown.

Laboratory feeding studies by Grundel (1994) showed that larvae fed pre-flowering, shade-grown lupine had higher growth rates than larvae fed post-flowering sun-grown lupine. Shading of sun-grown plants, however, did not affect development rates. In addition, this

Table 1. Nectar plant species used commonly by first and second brood Karner blue butterfly. Percent of all nectaring observations at a locality for all plant species used by more than 10% of the observed butterflies.

Plant species	Percent of butterflies nectaring at plant species								
First Brood	MI ¹	WI ²	WI ³	Locality WI ⁴		WI ⁵			
<i>Arabis lyrata</i>			50			11			
<i>Hedyotis longifolia</i>			14						
<i>Hieracium aurantiacum</i>					56				
<i>Lupinus perennis</i>					29	13			
<i>Melilotis officinalis</i>		16							
<i>Potentilla simplex</i>						35			
<i>Rubus flagellaris</i>	89	19							
<i>Rubus</i> sp.						20			
Second Brood	MN ⁶	MI ¹	MI ⁷	MI ⁸	MI ⁹	WI ²	WI ³	WI ⁴	WI ⁵
<i>Amorpha canescens</i>						15	39	16	
<i>Asclepias tuberosa</i>		66	40	22					
<i>Asclepias verticillata</i>							11		
<i>Berteroa incana</i>								23	
<i>Centaurea biebersteinii</i>				33	40				
<i>Euphorbia corollata</i>				33					11
<i>Euphorbia podperae</i>						12			
<i>Helianthus occidentalis</i>									13
<i>Liatris cylindracea</i>				11					
<i>Melilotus alba</i>						38			
<i>Monarda punctata</i>	91	20	20		60	13	25	13	
<i>Rudbeckia hirta</i>								28	
<i>Solidago speciosa</i>									17

References: 1 = Lawrence 1994, 2 = Leach 1993, 3 = Maxwell and Givnish 1993, 4 = Lane personal communication, 5 = Swengel 1993a, 6 = Lane 1994a, 7 = Papp 1993, 8 = Sferra et al. 1993, Site 1, 9 = Sferra et al. 1993, Site 2.

study indicated that larvae fed leaves from plants grown on sandy soils developed faster than those fed leaves from plants grown on soils with an A horizon, and they grew faster when fed leaves from plants with large scale infections of powdery mildew than plants currently bearing seeds. Lane (in preparation) found no difference in larval growth rates in laboratory feeding studies with sun- and shade-leaves from pre-flowering plants. Maxwell and Givnish (1993) reported that Karner blue abundance was positively correlated with the abundance of non-flowering lupine and negatively correlated with the abundance of flowering lupine. In 1995 studies, 75% of the larvae were found on non-flowering lupine (Maxwell and Givnish 1995). Feeding studies comparing flowering and non-flowering stems have not been done. Qualitative variation in lupine can affect Karner blue larvae, but the laboratory results need to be replicated and their significance extended to the field.

Swengel (1993b) compared larval abundance and body length to various lupine measurements to examine the relationship between lupine and larval phenology. The number of larvae was positively correlated with lupine rosette diameter, and larval length was positively correlated with lupine height (Swengel 1993b). These results imply that bigger lupine plants have more larvae, and the earlier lupine starts growth in the season, the longer the time the larvae have to grow and the bigger the larvae.

Lupine growth, reproduction, dispersal, and propagation. Lupine reproduces vegetatively and by seed. Seed pods have stiff hairs with an average of 4-9 seeds per pod (Boyonoski 1992). When seed pods are dry, they will suddenly twist and pop open (dehiscence), throwing seeds several feet. This is the only known dispersal mechanism and Celebrezze (1996) suggests that colonization would be very slow, about 0.5 to 2 meters per year (20 to 79 inches per year). Seeds are known to remain viable for at least three years (Zaremba 1991), do not have a physiological dormancy, and will readily germinate if moisture and temperature conditions permit. The hard seed coat produces an effective dormancy and germination is usually enhanced by scarification, stratification and/ or soaking in water (Boyonoski 1992, Zaremba and Pickering 1994, Welch, personal communication).

Lupine also reproduces vegetatively by sending up new stems from rhizomatous buds. Usually plants a few years old will form a clump of several stems and in areas with dense lupine it is difficult to distinguish individual lupine plants. Established lupine plants do not grow every year. It is not known how long an established plant can remain dormant.

Lupine can be propagated by planting seed or transplanting seedlings. Direct germination from seed appears to result in higher first year survival than seedling transplants (VanLuven 1994b, Zaremba and Pickering 1994). Seedling establishment from seed in New Hampshire was between 3-43 percent in the first year and survival of seedlings was about 50-60 percent per year (VanLuven 1994b). Large quantities of seed will be necessary to establish dense stands of lupine in this area. Welch (1994) established lupine patches with over 5,000, 8,500, and 17,500 2-4 month old seedlings and uncounted numbers of seeds near Waupaca, Wisconsin. The patches were established successfully, but no data are available on survival. Maxwell and Givnish (1994)

established lupine by direct seeding in experimental plots in 1993. Although soil preparation was homogeneous, lupine establishment was better in the compacted, subsided soils associated with an old trail. This area had less vegetative cover, and the lupine was growing in association with *Cycloloma atriplicifolium*, which may have protected it from deer browsing. During the dry 1995 season, *C. atriplicifolium* was absent and lupine on this trail developed faster and senesced earlier than the surrounding lupine, and lupine cover was greater where the seeded perennial grasses had established the best (Maxwell and Givnish 1996). These observations suggest that nurse plants may be useful for establishing lupine.

Renewal of lupine habitat. Lupine is an early successional species adapted to survive on dry, relatively infertile soils. Even very young seedlings have long tap roots that presumably allow the plant to reach soil moisture. It can grow on soils low in nitrogen because of its association with the nitrogen fixing bacterium *Rhizobium lupina*, and does not do well when grown without *R. lupina* (Zaremba and Pickering 1994). Similar to other legumes, it probably does best when growing on nitrogen-poor soils that have sufficient phosphorus. Lupine does not reproduce in dense shade. All available evidence suggests that lupine thrives on nitrogen-poor soils in partial- to open-canopied areas, and is suppressed by shade; it is possibly out-competed by other plants on nitrogen-rich soils, and phosphorus-poor soils.

Several species of pines, oaks, and shrubby vegetation are adapted to the same soils and habitat as lupine (Haney and Apfelbaum 1990, Nuzzo 1986), and without disturbances, they will close the canopy, shading and suppressing lupine (Apfelbaum and Haney 1991, Haney and Apfelbaum 1990). The rate of closure will vary from locality to locality, based on edaphic and prevailing climatic conditions, and current and historic management practices. If the habitat supports high grass and sedge productivity, then litter can build up that could also suppress lupine. Consequently, disturbances that reduce tree and shrub canopy cover are necessary for lupine to persist, and under some conditions, occasional disturbances that remove the litter layer are needed for lupine regeneration. Several disturbances have been suggested as beneficial for renewing lupine habitat, including prescribed fire, tree removal, and a variety of methods to kill tress and shrubs.

Other factors affecting lupine. Mechanical disturbance of the soil can affect lupine. Maxwell and Givnish (1996) evaluated the effect of tank traffic on plots of established lupine at Ft. McCoy, Wisconsin. This kind of traffic causes greater soil disturbance than ATV (all-terrain vehicle) traffic, but could be comparable to some of the traffic during site preparation and harvest of commercial forest stands. Tank traffic crushed the existing emergent lupine, and within several weeks, seedling germination was observed on the disturbed soil and the crushed plants regrew with a three-week delay in developmental phenology. In the following year, plants on the disturbed areas developed about two weeks faster than the surrounding

plants. Thus, mechanical disturbance can create greater heterogeneity in lupine development. As discussed below under microhabitat diversity, this heterogeneity can be beneficial to Karner blue.

Herbivory and disease may reduce the rate of canopy closure or open up gaps in the canopy. In this section, we review the direct effects of these factors on lupine; the indirect effects via canopy reduction are reviewed in the section on habitat below. Lupine is browsed by deer, woodchucks, and insects. The relationship between grazer density, grazing intensity, and Karner blue populations is largely unknown. If deer populations are too abundant in the spring and browse is scarce, excessive browsing could occur on lupine, with potential detrimental effects on Karner blue. Heavy spring flower browse by deer reduces the number of seed pods for that season's lupine (Straub 1994). Transplanted lupine may be less able to recover from being browsed than field sown plants (Zaremba and Pickering 1994). Herbivory by the painted lady butterfly (*Vanessa cardui*) has caused severe defoliation of lupine foliage (Lane, personal communication), but the potential detrimental effects on Karner blue are not documented. Lupine species typically contain alkaloid compounds which are hypothesized to serve as chemical defense mechanisms against herbivory (Dolinger et al. 1973), but the significance of these compounds in the ecology of Karner blue is not known. Several diseases of lupine are known, but their effects are unknown.

Nectar Food Resources. Adult Karner blue butterflies feed at flowers, sipping nectar and presumably obtaining nourishment; adult feeding increases longevity and fecundity in many Lepidopteran species, especially butterflies (Chew and Robbins 1989). Although increased longevity and fecundity have not been specifically demonstrated for Karner blue butterfly, it is generally agreed that nectar is an essential adult resource. Adult Karner blue butterflies spend considerable time nectaring on a wide variety of plant species (Appendix C). Adults have been observed during the first brood to feed on flowers of 39 species of herbaceous plants and 9 species of woody plants, and during the second brood on flowers of 70 species of herbaceous plants and 2 species of woody plants. Indeed, nectar plant availability may be a key factor in determining habitat suitability (Fried 1987). Lawrence and Cook (1989) suggested that the lack of nectar sources may limit populations at the Allegan State Game Area in Michigan, and Packer (1994) implicated the dearth of nectar sources as one of the causes of the extirpation of populations in Ontario. Bidwell (1994) found a positive correlation between nectar plant abundance, specifically abundance of *Monarda punctata*, and the number of Karner blue butterfly adults. Papp (1993) found a weak correlation between first brood adult numbers and nectar plant abundance, but no such correlation during the second brood. King (personal communication) did not find a correlation between adult Karner blue butterfly numbers and nectar plant abundance. Absence of correlation does not mean that nectar plants are unimportant, but suggests that other factors, such as larval density, are contributing more directly to adult population numbers.

Some plant species appear to be utilized more frequently than others (Bidwell 1994, Bleser 1993, Fried 1987, Lane 1994a, Lawrence 1994, Leach 1993), however experiments to assess adult feeding preference have not been conducted. The nectar plant used most frequently in the field may be the one that is spatially or temporally available or most abundant, and not the species that is preferred. Observations of nectaring frequency, however, can indicate the relative utility of the species as a nectar resource (Table 1).

In addition to nectaring, males and females sip at moist earth (mud-puddling) and human perspiration, and males sip at animal droppings (Swengel 1993a). Adults may be obtaining sodium or other substances from this behavior.

Microhabitats. Karner blue adults and immatures use a variety of microhabitats created by tree canopy cover, topography, and soil moisture, and the population dynamics of the butterfly is probably influenced by these factors. Adult butterflies use open-canopied areas for nectaring, roosting, mate location, and oviposition (Lane 1994a, 1994b, Lawrence 1989, 1994, Maxwell and Givnish 1993, Packer 1987). The majority of Karner blue nectar plants require medium to high levels of sun to produce flowers and the adults nectar most frequently in open-canopied areas. The phenology of flower production is also likely to vary with microhabitat and microhabitat diversity may provide a more guaranteed source of nectar by enabling many potential nectar plant species to coexist in the habitat. For example wetlands adjacent to suitable Karner blue habitat at Indiana Dunes National Lakeshore or Necedah Wildlife Refuge may provide almost unlimited nectar resources. Extremely xeric sites, on the other hand, such as Allegan State Game Area, may have limited adult nectar resources which could limit butterfly populations (Lawrence and Cook 1989).

Adults are commonly found in open-canopied areas. In Minnesota, Lane (1992a) classified habitats with lupine or adult butterflies, and showed that adults were found in areas with less than 5 percent canopy cover. In western Wisconsin, Maxwell and Givnish (1994) collected data on the physical structure of habitat and cover estimates of selected vegetation, and found a positive correlation between adult Karner blue butterfly abundance and grass cover. Because the grass was used as adult roosting sites, they suggested that this indicated the importance of roosting sites for healthy populations of Karner blue. Grass cover may also indicate open canopy on less xeric, slightly more fertile areas of savanna, which could be beneficial in other ways to Karner blue.

Specific adult behaviors are commonly seen in open-canopied areas. Adults have been observed roosting in open- to closed-canopied areas during the day on several woody and herbaceous plant species, but at night adults have been seen roosting in the open on grasses such as big bluestem (*Andropogon gerardii*) (Schweitzer 1989). Male Karner blue butterflies appear to search for mates predominantly in open-canopied areas. Males are commonly observed in open areas, and in studies on butterfly movement, Bidwell (1994) commonly observed males flying back and forth through open areas.

Females have been observed ovipositing in open- to closed-canopy and in a variety of slopes and aspects (Lane 1993, 1994c, Maxwell and Givnish 1993). Females may be ovipositing in open- and partial-canopied areas in response to the greater lupine abundance in these microhabitats. In addition, in cool weather open and sunlit areas may permit butterflies to achieve threshold temperatures needed for flight activity (Lane 1994c). Shaded or closed-canopied areas may provide for cooling on extremely hot days (Lane 1994c, Packer 1994). Egg deposition in a variety of microhabitats may also serve to mitigate physical or biological risks to immature stages (Bidwell 1994, Lane 1994c). For example, several researchers have suggested that lupine senescence is earlier in xeric open canopied areas and may result in larval starvation, particularly in drought years.

Optimal microhabitat for immature stages may contrast with that used by adults (Savignano 1990, Spoor 1994, Lane 1994b). Studies of larvae in Minnesota and Wisconsin, showed significant differences in larval survival and ant-tending between microhabitats (Lane 1994b). For second brood larvae, survival was highest in closed-canopied areas, intermediate in partial-canopied areas, and lowest in open-canopied and very xeric areas (Lane 1994b). Although the cause of mortality is uncertain, the lupine plants were heavily infested with powdery mildew (possibly reducing quality) and the introduced predator, the seven spotted lady beetle (*Coccinella septempunctata*) was observed on lupine (Schellhorn et al. unpublished). Lawrence and Cook (1989) suggested that the highest quality lupine plants for larvae occur in areas with partial sun, which is consistent with Grundel's (1994) finding that larvae fed post-flowering, shade-grown lupine had higher growth rates than larvae fed post-flowering sun-grown lupine.

In closed-canopied areas larvae may be more protected from temperature extremes, wind and rain, or natural enemies. Natural enemies may either not inhabit these areas or be less efficient at searching. Although the proportion of older larvae tended by ants was similar in open- and closed-canopy areas, early instar larvae were tended more in partial-canopy areas (Lane 1994b). Moreover, the tending ant species were different in the different microhabitats (Lane, personal communication). At Ft. McCoy during 1995, the summer drought conditions resulted in early senescence of lupine (Maxwell and Givnish 1996). In open-canopied areas, late-maturing second brood larvae were often seen on completely senesced plants, while in shady areas senescence was delayed. Karner blue populations declined during this generation and were more abundant in the shade, and the authors suggest that early lupine senescence may have been the cause.

In summary, mating and adult feeding take place primarily in open-canopied areas. Oviposition occurs in many types of microhabitats, but larval growth and survival may be best in partial- to closed-canopy areas. Small-scale variation in topography and soil moisture could be beneficial to Karner blue. A highly variable microtopography creates a highly variable thermal environment and a highly variable plant community and canopy structure, and variation in soil moisture will also contribute to variation in plant community and canopy structure. In addition, such variation in plant community and canopy could be beneficial to Karner blue in the long-term because in hot, dry years Karner blue can be found using shady, moist microhabitats, while in cool years,

they are more strongly associated with sunny and partially sunny microhabitats.

Associated Ants. Immature stages of the Karner blue butterfly have a mutualistic relationship with ants. Larvae tended by ants have a higher survival rate than those not tended (Savignano 1990, 1994a), presumably because the ants provide some protection from larval natural enemies. Larvae possess specialized glands which secrete a liquid that is avidly harvested by ants, probably containing carbohydrates and amino acids. Tending levels for late instar larvae are close to 100 percent. In most cases, however, very few early instars are tended (Lane 1994b, Savignano 1990). Several ant species have been observed to tend Karner blue larvae (Table 4). Some species of ants appear to provide greater protection than other species. For example, larvae last tended by *Formica lasiodes* had significantly higher survival than those last tended by other ant species (Savignano 1990, 1994a).

During pupal survival studies, Lane (unpublished) observed several ant species to be associated with Karner blue pupae. One species of ant built nests of dead vegetation around the pupae. Many of the pupae within these nests were observed to eclose but how the ants influence pupal development or survival is not clear.

At the Crossgates Mall site in NY, Spoor (1993) observed ants (*Myrmica* sp.) removing eggs of Karner blue from lupine stems. Removal rates were sometimes exceedingly high (39-74 percent missing in one series of observations). Whether these eggs were killed or reared by the ants is unknown.

Table 2. Ant species tending Karner blue butterfly larvae.

Ant Species	Locality	Reference
<i>Aphaenogaster rudis</i>	Ont	Packer (1990)
<i>Camponotus americanus</i> Mayr	NY	Savignano (1994)
<i>Camponotus ferrugineus</i>	WI	Bleser (1992)
<i>Camponotus novaeboracensis</i> Fitch	NY	Savignano (1994)
<i>Camponotus pennsylvanicus</i>	Ont	Packer (199)
<i>Crematogaster ashmeadi</i>	WI	Bleser (1992)
<i>Creatogaster cerasi</i> Fitch	NY	Savignano (1994)
<i>Dolichoderus</i> (<i>Hypoclinea</i>) <i>plagiatus</i> Mayr	NY	Savignano (1994)
<i>Formica difficilis</i> Emery	NY	Savignano (1994)
<i>Formica exsectoides</i>	Ont	Packer (1990)
<i>Formica fusca</i>	WI	Bleser (1992)
<i>Formica lasioides</i> Emery	NY	Savignano (1994)
<i>Formica montana</i>	WI	Bleser (1992)
<i>Formica</i> (<i>Neoformica</i>) <i>incerta</i> Emery	NY	Savignano (1994)
<i>Formica</i> (<i>Neoformica</i>) <i>nitidiventris</i> Emery	NY	Savignano (1994)
<i>Formica</i> (<i>Neoformica</i>) <i>schaufussi</i> Mayr	NY	Savignano (1994)
<i>Formica querquetulana</i> Wheeler	NY	Savignano (1994)
<i>Formica schaufussi</i>	WI	Bleser (1992)
<i>Formica subsericea</i> Say	NY	Savignano (1994)
<i>Lasius alienus</i> Foerster	NY	Savignano (1994)
<i>Lasius neoniger</i> Emery	NY	Savignano (1994)
<i>Monomorium emarginatum</i> DuBuois	NY	Savignano (1994)
<i>Myrmica americana</i> Weber	NY	Savignano (1994)
<i>Myrmica fracticornis</i> Emery	NY	Savignano (1994)
<i>Myrmica punctiventris</i>	Ont	Packer (1990)
<i>Myrmica sculptilis</i>	NY	Savignano (1990)
<i>Paratrechina parvula</i> Mayr	NY	Savignano (1994)
<i>Tapinoma sessile</i> Say	NY, WI	Bleser (1992), Savignano (1994)
<i>Tetramorium caespitum</i>	WI	Bleser (1992)

Although ants appear to be important in the life cycle of Karner blue, it is uncertain if it is necessary to manage habitat to ensure their presence. The interaction between Karner blue and ants appears to be facultative, and the ants appear to be opportunistic in tending, so that any species that is present might tend the larvae and pupae. In contrast, the apparent variation in protection provided by different ant species could influence Karner blue abundance and population dynamics, and therefore methods to manage the habitat to encourage more beneficial ant interactions may merit consideration.

Dispersal. Nearly all researchers that have examined Karner blue dispersal have concluded that dispersal rates and distances for the butterfly are relatively low and short (Bidwell 1994, Fried 1987, King 1994, Lawrence 1994, Schweitzer in Givnish et al. 1988, Welch 1993). King (1996), however, measured a maximum dispersal distance of <3 kilometers (<1.8 miles) and 92.5% moving less than 1.5 kilometers (0.9 miles). Prior to this result, many believed that dispersal was extremely rare and short, with nearly all movement <200 meters (220 yards). Although King's (1996) results expand the spatial scale of dispersal by an order of magnitude, the inferred rates are still relatively low and short.

Unfortunately, there has been no critical re-examination of the methods and the data. Without clear information on the sampling intensity at different distances from the release points, it is difficult to interpret the results. Definitive studies on insect dispersal frequently uncover unanticipated high frequencies of movement and distances far greater than expected. It is unknown what intrinsic factors or environmental conditions stimulate dispersal between habitat sites, or whether all Karner blue movement is trivial (movement that is associated with seeking food, mates, etc.) rather than migratory (movements where individuals do not respond to food or mate stimuli). Currently, much of the habitat between occupied areas is unsuitable for Karner blue. In some cases this is because the intervening habitat has been destroyed by development (such as in some areas of New York and New Hampshire). In other cases the historic extent and connectivity of suitable habitat is not clear.

Dispersal has not been carefully defined in the Karner blue literature. It usually refers both to the movement of individuals within and between suitable habitat sites. Because these two types of movements have different ecological implications, they will be separated in this discussion. The movement of individuals away from their natal site of suitable habitat, leaving the site and potentially finding another site will be referred to as dispersal from sites and includes dispersal between habitat sites. Movement that remains in a habitat site (or within the local population) will be called within habitat movement. Because suitable habitat sites vary in size, the frequency of these types of movement will vary from site to site. Dispersal from sites may lead to recolonization events, while movement within sites may result in greater use of the site, but will not contribute to recolonization.

The primary methods that have been used to determine dispersal distances and rates for the Karner blue butterfly are mark-release-recapture (MRR) (Bidwell 1994, Fried 1987, King 1994, 1996, Lawrence 1994, Schweitzer in Givnish et al. 1988) and tracking of individual butterflies (Welch 1993). Given their small size and that only a small number of butterflies can be found dispersing, mark-release-recapture methods have been the most cost-effective method of obtaining information on dispersal. Because MRR methods rely on detecting the rare long-distance recapture and a sampling intensity that declines with distance, they tend to underestimate the number and distance traveled by dispersing individuals. In addition, dispersal distance and rate may be related to the age of the insect (younger, prereproductive adults may be more migratory than older, reproductive adults). Some researchers have suggested that MRR

methods injure the insects (Murphy 1988), but extensive MRR work on Karner blue butterfly by an experienced researcher indicated that debilitating injury occurred to less than 1 percent of all individuals processed (Schweitzer 1994a); the effect of marking on dispersal behavior is not known. Morton (1989) found that high recapture frequencies and good fits to Poisson distributions are unreliable indicators of the suitability of the MRR technique for measuring dispersal, and the suitability of MRR techniques for estimating dispersal in Karner blue has not been rigorously examined. Given the dearth of information on dispersal of Karner blue and the limitations of alternative methods, MRR methods will likely provide the best insight into dispersal of Karner blue. None of the dispersal information has been summarized to provide an estimate of the functional relationship between distance and the probability of dispersal.

Dispersal from sites. Most studies on Karner blue butterfly have documented very few between habitat dispersal events (Bidwell 1994, Fried 1987, King 1994, Lawrence 1994, Schweitzer in Givnish et al. 1988). King (1996) documented the greatest amount of between site dispersal. This study was conducted at the Necedah National Wildlife Refuge in the Glacial Lake Wisconsin recovery unit. The three occupied sites are each about ~100 hectares (~200 acres), and are separated from each other by >1,000 meters of mostly open wetlands habitat. Using MRR methods, an estimated 11 percent of the individuals moved between sites during the second flight, with the greatest emigration from the lowest density site (King 1996). In New York during 1975, Schweitzer (personal communication) captured two individuals out of about 50 individuals marked at a much smaller site about 1.3 kilometers away. Schweitzer (personal communication) measured little dispersal in the Concord, New Hampshire population. Less than 1 percent of the marked individuals crossed a narrow, little-used road separating two large habitat patches. Fried (1987) captured only three individuals (total captured = 224) dispersing between three sites that were approximately 400 to 700 meters apart. The habitat matrix between Fried's study sites was primarily dense woods or low shrubs, although dirt paths connected them. In Wisconsin, Bidwell (1994) captured 21 individuals (total number marked = 724) dispersing between habitat sites. Two sites were only 50 m apart, but they were separated by a dense stand of birch. These two areas were approximately 1,200 to 1,600 meters from a third habitat site. Fourteen of the 21 dispersal events recorded were between the two close sites and five were between these and the farther site. The remaining two dispersers were recaptured between the habitat sites. Maximum distances recorded by Bidwell (1994) were 1,600 meters for a male and 1,195 meters for a female. In Michigan, Lawrence (1994) marked 538 individuals and recaptured 142. His five study sites were 0.5 to 2.5 kilometers apart. No individual was recaptured at a site other than at the original marking site. Lawrence suggested that between habitat dispersal was probably uncommon because they marked and recaptured frequently, which would have enabled them to observe such dispersal if it were common.

Another approach used to determine dispersal distance is to follow individual Karner blue butterflies (Welch 1993). Potentially dispersing butterflies were located by searching areas 200 meters from lupine sites. The number of potential dispersers and distance each moved was recorded for spring and summer flights, along with wing-wear (fresh and worn individuals), sex, and habitat types (open and closed canopy). A total of 78 butterflies were observed. The largest

number of potential dispersers were fresh males in open habitat during the first flight. Numbers of potential dispersers were lower for both sexes, wing-wear classes, and habitats during the second flight. Observed dispersal distances were farthest for fresh males in open habitat, ranging from 65-1,350 meters and averaging 461 meters. Dispersal distances for females were farther for worn individuals. Distances range from 85- 565 m in open habitat with an average of 244 meters. These data have not been statistically analyzed.

The percent of marked individuals dispersing between suitable habitat sites varied from 0 (Lawrence 1994) to 2.4 and 2.9 percent (Bidwell 1994, Fried 1987) or less than 5% (Schweitzer 1994a) to 11 percent (King 1996). In studies on the Heath fritillary butterfly (*Mellicta athalia*) in England, Warren (1987) found an average of 1.5 percent dispersal between habitat areas. He argued that if similar rates of dispersal were observed to other areas not sampled, that a fairly substantial proportion of adults may be emigrating from the populations studied and arriving at new habitat areas (Warren 1987). For Karner blue it is unclear if observed rates of between habitat dispersal will limit recolonization of suitable habitat in all habitats, but the dispersal rates observed at Necedah National Wildlife Refuge indicate that recolonization is probably extensive.

Many factors have been suggested to be dispersal barriers for Karner blue butterflies. Anecdotal evidence has indicated that many geographic, vegetational, and human-constructed structures might act as dispersal barriers, including four-lane highways with heavy traffic in urban or semiurban areas, steep embankments and cliffs, forested areas if no openings such as trails or roads are present, and residential and commercial areas (including paved parking lots and roads), but scientific evidence supporting any of these speculations is absent.

Movement within sites. Within habitat movements were also examined in the above MRR studies and by following individual butterflies. The distance between the majority of recaptures was less than 200 meters for both Lawrence (1994) and Bidwell (1994). In examining the distances moved by marked individuals in one day, King (1994) also reported movement distances of less than 200 meters with the majority moving 25-50 meters. In the larger Indiana Dunes Inland marsh site, Knutson (1995) reported a maximum observed movement distance of 312 meters, which was less than the 850 meters possible in that site.

Lane (1994a) measured within habitat flight distances by following individuals and marking all landing points. The average flight distance between points was 4.99 meters for males and 1.49 meters for females, i.e. most within habitat flights were short distances, but adults took many small flights in a day (Lane 1994a). These data are not readily extrapolated. The overall picture that emerges is that within sites Karner blue moves short distances and moves often.

Dispersal corridors. Little data exist regarding dispersal corridors for Karner blue. It is widely believed that open-canopied corridors through wooded areas provide Karner blue with a dispersal corridor, but except for anecdotal observations, this has remained unproven. Welch (1993) conducted the most extensive recorded observations of Karner blue butterflies in flight. He found

that dispersing butterflies almost always followed canopy openings along fence rows, woodland trails, or small gaps in the canopy, stopping frequently to bask in the sun. During these between-site movements open-canopied areas may be needed for thermoregulation (Lane 1994c), orientation (Welch 1993), or both. Thus, dispersal corridors may be quite diaphanous in native habitat, formed by a network of partially connected canopy gaps and trails. Of the 78 butterflies observed by Welch (1993), only two did not exhibit this common pattern of dispersal. One of these flew up the oak canopy dispersing above the canopy, and the other flew through the shade of a full canopy. Schweitzer (1979) also observed some adults to move over a young forest canopy. The frequency of these unusual dispersers is not known.

Habitat/Ecosystem

Structure. The physical features that affect Karner blue habitat vary across its geographic distribution. The western part of the range is subject to greater continentality effects, which include greater annual variation in temperature, lower precipitation, and greater year-to-year variation in precipitation. Average annual precipitation is higher in the eastern part of the range at over 50 inches per year and drops off in the west to under 40 inches per year. Annual variation in precipitation is generally less than 10 percent of normal in the east, but more variable in the west at 15 percent of normal. In the east, the annual range in temperature is less than 28°C, but in the west the annual range is greater than 28°C. Thus, in the west Karner blue habitat will be subjected more frequently to drought and temperature extremes, such as cool springs or hot summers, than in the east.

Throughout its range, Karner blue butterfly was historically associated with native barrens and savanna ecosystems, but it is now associated with remnant barrens and savannas, highway and powerline right-of-ways, gaps within forest stands, airports, and military camps that occur on the landscapes previously occupied by native barrens and savannas. Almost all of these contemporary habitats can be described as having a broken or scattered tree canopy from 0 to between 50 and 80 percent canopy cover, with grasses and forbs common in the openings. The habitats have lupine, the sole larval food source, nectar plants for adult feeding, critical microhabitats, and attendant ants. The stature and spacing of trees in native savannas is somewhat variable, reflecting differences in soils, topography and climate (Nuzzo 1986), and the distribution of trees in contemporary habitat is similarly diverse. Soils are typically well drained sandy soils which influences both plant growth and disturbance frequency. These conditions are generally wet enough to grow trees but dry enough to sustain fires (Breining 1993). Topography is diverse and includes flat glacial lake beds, dune and swale lake shores, and steep, dissected hills.

Remnant native habitats. Barrens are often separated from savannas on the basis of soil type, plant species and form, fire frequency, etc., however, the classification is not consistent among systems. For example in the Midwest Oak Ecosystems Recovery Plan, barrens are considered to be a treeless type of savanna, and by this definition, most Karner blue habitat would be considered savanna, but not barrens. In other parts of the Plan, savannas are wet/mesic habitats

with burr oak and other mesic oak species, while barrens are xeric with 20-80% canopy cover on sandy soils. On the other hand, Karner blue habitat in Minnesota is classified as dry oak savanna, barrens subtype (MN DNR 1993). Given the lack of a generally accepted classification system, any of the following terms will be used to describe the types of ecosystems providing habitat for the Karner blue.

Most of the eastern portions of Karner blue habitat are dominated by pitch pine (*Pinus rigida*), scrub oak (*Quercus ilicifolia*), or both. This ecosystem has been referred to as the pitch pine barrens, Northeast pine barrens, or (Albany) pine bush (Dirig 1994, Schweitzer and Rawinski 1987). Karner blue habitat around Saratoga, NY, however, appears to resemble oak savanna (Schweitzer 1990).

In the midwest, black oak (*Quercus velutina*), white oak (*Q. alba*), pin oak (*Q. ellipsoidalis*), bur oak (*Q. macrocarpa*), jack pine (*Pinus banksiana*), or any combination of these four dominate suitable Karner blue habitat. Composition can vary from predominantly oak, especially black or pin, to mixtures of oak and jack pine, to predominantly jack pine. Black and pin oak dominated communities have been classified by Curtis (1959) as oak barrens. Those dominated by black oak, with or without white oak and jack pine, will be referred to as oak barrens. Sites dominated by jack pine, such as portions of central and northwest Wisconsin where prescribed burns have not eliminated the pines, are called jack pine barrens. In this document "oak and pine barrens and savanna" will refer to all the above types.

Some of the common species found in the understory of these barrens and savanna habitats are big bluestem grass (*Andropogon gerardii*), blueberry (*Vaccinium angustifolium*), little bluestem (*Schizachrium scoparium*), Indian grass (*Sorghastrum nutans*), butterfly weed (*Asclepias tuberosa*), sweet fern (*Comptonia peregrina*), spotted knapweed (*Centaurea maculosa*), *Rubus* spp., soapwort (*Saponaria officinalis*), bee balm (*Monarda fistulosa*), bracken fern (*Pteridium aquilinum*), New Jersey tea (*Ceanothus americanus*), and goat's rue (*Tephrosia virginiana*) (The Nature Conservancy, in preparation).

Dune and swale habitats are one of the most biologically diverse in the Great Lakes Basin (Rankin and Crispin 1994), originally extending along the shore of Lake Michigan from southern Wisconsin through the Chicago and Gary metropolitan areas and north into southwestern Michigan. The dunes are in close proximity to the swales, creating an extreme diversity of regularly alternating microhabitats from xeric, sandy upland habitats to wetlands, and back to uplands and again to wetlands over distances of less than 50 meters. Karner blue populations can be found in the uplands, which are oak barrens habitats, but adults will forage on nectar-producing plants in the adjacent wetlands.

Contemporary anthropogenic habitats. Karner blue also occurs in many habitats dominated by anthropogenic activities. These include powerline and highway rights-of-way, vegetation surrounding airport runways, young commercial forest stands, open areas within developed

commercial forest stands, military bases, and many other such areas. These areas all have soils that are suitable for lupine growth, an open canopy, and management that causes soil disturbance or suppression of perennial shrub and herbaceous vegetation (such as by mowing, brush-hogging, chemical control, or prescribed fire). These habitats are very diverse vegetationally, and often have many of the herbaceous species that co-occur with lupine in the native remnant barrens and savanna habitats.

Renewal of Habitat for Karner Blue. Karner blue habitat is maintained in the balance between its decline from canopy closure and its renewal from external disturbance. Natural disturbances, such as fire (Clark 1988) and large animal grazing (Hobbs and Huenneke 1992), that open canopy have decreased since the time of European settlement, so this balance is largely maintained by management activities (refer to Appendix G). These management activities intervene to influence the rates at which suitable habitat declines in quality and is renewed. Thus, an understanding of both natural factors and the interaction with management is essential to understanding the maintenance of Karner blue habitat. It is likely that the gradients in temperature and precipitation that occur from the eastern to western part of the range of Karner blue butterfly affect these rates. In the drier, more variable climates of the western part of the range, it might be predicted that rates of canopy closure will be slower and rates of natural renewal, such as fire will be faster, which would have resulted in a natural landscape with more early successional barrens and savanna, and healthier Karner blue populations.

Many ecological processes act on Karner blue habitat to maintain populations of the butterfly. In the native barrens and savanna habitats, many factors, including deliberate fire, wildfire, disease, such as oak wilt, and herbivory, probably interacted to maintain the native vegetation and the associated Karner blue populations. In habitats dominated by anthropogenic activities, many management activities probably have been inadvertently beneficial to Karner blue butterfly. In general, the relation between specific management practices and Karner blue populations is not well characterized, yet the persistence of Karner blue on these managed ecosystems, suggests a basic compatibility between Karner blue and alternate land uses that would merit additional study (refer, for example, to Forest Management Guidelines, Lane 1996).

Prescribed fire and targeted removal or suppression of trees and shrubs are methods commonly suggested for renewing Karner blue habitat, and they will be discussed separately below.

Remnant native habitats. The native barrens and savanna ecosystem and its unique combination of species developed from the interplay of natural disturbance processes, edaphic factors, climate, etc. (Faber-Langendoen 1991, Forman 1979, Tester 1989). Fire is recognized as the key element maintaining savanna vegetational structure and species composition (Faber-Langendoen 1991, Haney and Apfelbaum 1990, Tester 1989, Wovcha et al. 1995). Fire influences ecosystem dynamics by decreasing soil nitrogen and organic matter and raising pH (Tester 1989). It exposes mineral soils and reduces woody plant cover, conditions required by many savanna adapted species (Payne and Bryant 1994), and clears the understory but does not eliminate the adapted tree species. These trees survive by resisting fire with thick barks, by resprouting, or by

germinating seeds after disturbance by fire. These set-backs of the woody vegetation maintain a mixture of open- to densely-canopied patches of habitat (Nuzzo 1986, Shuey 1994). Fire suppression in recent history has resulted in succession of these barrens and savannas to woodlands.

Mammalian grazing, burrowing, trampling, etc., are considered by some to be a critical element in maintaining the oak savanna ecosystem (Hobbs and Huenneke 1992, Swengel 1994). Elk (*Cervus elapsus*) and bison (*Bison bison*) are likely to have once grazed and browsed in Minnesota and Wisconsin (Hamilton and Whitaker 1979, Jackson 1961). During spring, elk feed extensively on grasses, sedges, and weeds. During summer, grasses, shrubs and trees are eaten, and the diet shifts solely to shrubs and trees during fall. Bison feed on species similar to those consumed by domestic cattle, primarily grasses. Deer browse and occasionally graze on legumes and other selected plants. Deer are at very high population levels (for example, an average of 20 deer/sq. mi., and 60-80/sq. mi. in the Whitewater Wildlife Management Area in Minnesota, Jon Cole personal communication) at some sites with Karner blue. Browsing by deer probably has helped to maintain the open canopy that is characteristic of savanna by killing or suppressing tree seedlings. In some areas browsing is so high on oak and jack pine seedlings and selected herbaceous species that several age classes of trees are missing (Lane, personal communication). If browsing by deer continues at these levels, regeneration of trees will be insufficient to maintain savanna. Similarly, deer grazing may reduce reproduction and survival of herbaceous plant species, such as lupine (Packer 1994, Schweitzer personal communication, Straub 1994).

It is possible that extirpation of bison and elk and increased numbers of deer have resulted in changes to the structure and species composition of the remnant barrens and savanna ecosystem. At the Whitewater Wildlife Management Area, grass litter has accumulated in open areas and certain age classes of trees are missing. In Ontario, extremely high deer populations consumed from 30% to 90% of the lupine plants in some areas, and probably contributed to the extirpation of the Karner blue butterfly (Boyonoski 1992, Packer 1994, Schweitzer 1994b).

Soil disturbances created by small mammals, such as plains pocket gopher (*Geomys bursarius*), can also affect the composition and abundance of oak savanna plant species (Reichman and Smith 1985, Davis et al., in prep.). For example, the savanna herb *Penstemon grandiflorus* (Scrophulariaceae) has increased growth rates and earlier reproduction when growing on areas disturbed by the northern plains gopher (Davis et al. in preparation). Lupine germination and growth on gopher mounds has not been studied, however the early successional disturbance-associated niche of lupine suggests that it might benefit from gopher disturbances.

Insects and diseases that remove canopy trees have also contributed to the persistence of barrens and savannas in the central United States. Many high quality oak savanna remnants are in areas where canopy trees have died as a result of oak wilt (*Ceratosystis fagacearum*). Two-lined chestnut borer (*Agilus bilineatus* Weber), jack pine budworm (*Choristoneura pinus* Freeman),

and gypsy moth (*Lymantria dispar* L.) are likely to reduce canopy cover in over-grown barrens areas (Coulson and Witter 1984).

Soil type and topography have contributed to the maintenance of barrens and savanna species composition and structure. The sandy, well-drained soils characteristic of Karner blue habitat retain little moisture. These xeric conditions reduce growth of woody species (Burns and Honkala 1990, Klaus Puettmann, personal communication), and only species tolerant of these conditions persist. In combination with soil type, many savanna species owe their persistence to topographic effects, especially in the unglaciated driftless regions in Wisconsin and Minnesota (Lane 1994a, Wilde 1948). The steep slopes exhibit natural slumping, creating exposed mineral soil that favors early successional species. Many of these slopes are south and southwest in aspect, further enhancing their xeric quality and resulting in further suppression of woody plant species. In addition, during spring snow melt and summer rain storms, several valleys experience erosion, exposing the mineral soils that benefits early successional species, such as lupine.

Contemporary anthropogenic habitats. Silvicultural practices can have beneficial or detrimental effects on Karner blue, many of which are summarized in Lane (1997). For example, in some parts of Jackson, Juneau, Wood, and Burnett counties in Wisconsin, summer harvest, road building and maintenance, site preparation, tree planting, slash burning, and other activities may have been beneficial to lupine and Karner blue. Within this complexity of management activity, however, it is important to focus on how various practices affect the balance between local extirpation of butterflies in a stand and recolonization of stands by butterflies. Silvicultural practices disturb habitat and butterflies in ways that can be related to the type of disturbance (mechanical, chemical, or prescribed fire), its spatial extent (area affected), its intensity (direct effect on the soil, lupine, and Karner blue), and seasonal timing (phenology). The effects of these management practices will be quite diverse, but these effects can be categorized as direct effects on populations of the butterfly, effects on important plant species, such as lupine, nectar plants, and competing plants, and effects on the soil that influences these plant responses. All of these effects will depend on many habitat characteristics, such as the spatial distribution and abundance of plant resources, site quality, and topography, the previous history of the site, and the recent history of management. Because there is little scientific information for using silvicultural practices to enhance Karner blue butterfly, management planning should take an adaptive management approach. This will require that clear goals be set that include Karner blue butterfly, observations be taken before and after implementation of management, and practices modified based on the observations.

Because silvicultural practices are implemented to achieve multiple management goals, there will be inevitable tradeoffs between achieving the various goals. For example, at a particular site, a manager may desire maximum immediate financial returns, minimal risk on investment, maximum sustained yields, optimal wildlife game animal production, and increased Karner blue butterfly populations. In most cases it will not be possible to optimize simultaneously all economic and wildlife goals. Instead, it will be necessary to understand which silvicultural practices are compatible with each of these many possible goals and which practices create

tradeoffs among them. For some managers, such compatible practices may be those that, for example, enable sufficient financial return while supporting sufficient butterflies. Understanding how silvicultural practices affect both economic and butterfly needs will be challenging. One possible approach is to evaluate silvicultural practices by commodity [Bill, do you agree, or is there a better way to subdivide silvicultural forms?]. A pine stand managed for saw timber will typically be on better soils, under more intensive timber management, and be planted at higher density, be more valuable on a per acre basis, and take longer to mature compared to a pine stand managed for pulp production. These factors suggest that there will be different suites of tradeoffs associated with each production system. [Bill, can you provide an example to make this more realistic?] Appropriate management for Karner blue on silvicultural lands should recognize potential variation in compatibility when assessing the effects of a silvicultural landscape on populations of Karner blue. Considerable efforts should be extended to understand the complexities of management and their consequences for Karner blue butterfly in working silvicultural landscapes.

Silvicultural practices continually evolve as demand and technology changes. For example, because red pine fiber is now preferred to jack pine fiber in pulp processing, there has been a shift to replacing jack pine plantations with red pine plantations in many commercial forests. The effect of this shift on Karner blue butterfly is not known, but because red pine has a denser canopy at similar stand densities and is grown on a longer rotation than jack pine, this shift may be detrimental to Karner blue butterfly. The effects of these changes in silvicultural practices on Karner blue should be evaluated carefully through an adaptive management process.

Understory legumes, such as lupine, can raise soil nitrogen levels, improve rates of mineral cycling, reduce surface runoff and soil erosion, and may improve soil organic matter content, soil structure, and cation exchange capacity, and inhibit soil-borne pathogens (Smethurst et al. 1986, Turvey and Smethurst 1983). Many of these effects would benefit forestry production. The main cost might be the potential competition between lupine and the establishing trees. Thus, in many situations it may be beneficial for production goals to encourage the growth of existing lupine and associated Karner blue butterflies, as long as it was not necessary to incur the cost of planting lupine.

Military training activities may have been beneficial to Karner blue. The Fort McCoy Military Reservation contains some of the largest populations of Karner blue in Wisconsin (Bleser 1994, Leach 1993), where over 97% of the patches of lupine on the property are occupied by Karner blue. Larsen and Wilder (1994) have hypothesized that military training activities, particularly inadvertent fires caused by artillery and mechanical disturbance by tracked vehicles, have created a mosaic of successional states similar to those in native habitats. Comparative studies relating the intensity of training activities to the density of butterflies suggest that these activities have indeed been beneficial to Karner blue (Bidwell 1994). Maxwell and Givnish (1995) initiated

experiments to determine whether fire and tracked vehicle traffic have beneficial effects on Karner blue. Results are still preliminary, but tracked vehicle traffic does create microsites where lupine germinates in profusion (Maxwell and Givnish 1995, 1996).

Maintenance of suitable Karner blue butterfly habitat on rights-of-way and near airport runways has not been systematically studied, but it is appropriate to focus on how management practices affect the balance between local extirpation of butterflies at a site and recolonization of sites by butterflies. Because of incomplete scientific knowledge, management of these areas will require adaptive management. Broad-scale applications of broad-spectrum herbicides can be detrimental to existing lupine in these habitats, but could be beneficial if they suppress lupine competitors and enable lupine to establish. Spot applications of more selective herbicides and mechanical suppression of woody plants may be more beneficial to existing lupine and Karner blue butterfly. Building, mowing, and grading activities in rights-of way may have beneficial effects on lupine and butterflies, but the effects may depend on the scale and timing of the activity.

Prescribed fire. Among the possible disturbances, fire has been widely regarded as an effective and efficacious means to reduce canopy cover and the litter layer, thereby maintaining an early successional habitat suitable for growth of lupine in native barrens/savanna ecosystems. Not all fires are effective at reducing canopy cover. A wildfire in 1986 at the Indiana Dunes National Lakeshore top-killed most oaks, but within several years the heavy resprouting from the oak roots resulted in a very dense shrub-like canopy (Martin 1994). The prescribed fires at Ft. McCoy did not reduce canopy cover (Maxwell and Givnish 1996); indeed, oak wilt caused greater canopy reduction in this area than the prescribed fires.

The direct effects of fire on lupine are partially understood. In general, it is expected that fire will release lupine from shade-suppression, but the immediate effects of fire on existing plants and the seeds may be positive, negative, or neutral. At the Oak Openings in Ohio, the short term effects of a moderate-intensity fire on established lupine plants were increased vegetative growth, flowering, and seed set (Grigore 1992). However, at least 95 percent of the seeds on the soil surface and new seedlings were killed. Seeds buried in the soil germinated at similar rates as those in unburned plots (Grigore 1992). At Ft. McCoy in Wisconsin, the occurrence of established lupine was not significantly affected by fire; lupine flowering declined on all plots, but the number of inflorescences declined less in the burned treatments than in the unburned control plots (Maxwell and Givnish 1996). The authors suggested that reduced competition and/or nitrogen volatilization may have resulted in increased germination in previously unoccupied areas. Both of these studies indicate that burning may enhance flowering of established plants, and the meager data suggest that germination of surviving seeds is not affected by moderately intense burning.

Fire may affect Karner blue by long-term improvements in habitat quality or by causing direct mortality to individuals present at the time of burning. It is expected that fire will reduce Karner blue populations during a relatively short period immediately after a fire, but that afterwards the population will increase to levels higher than those in the pre-burn habitat (Givnish et al. 1988).

Available evidence, summarized below, supports the first part of this prediction, but there is no data that addresses adequately the second part of the prediction.

Research to date suggests that adult numbers can be reduced and eggs and larvae present in burned areas will be killed by fire (Grundel 1994, Maxwell 1996, Maxwell and Givnish 1994, Swengel 1993a). Eggs and larvae do not survive fire, but they can survive in habitats that are burned. Larvae found in the generation immediately after a fire were all in unburned portions of study sites (Bleser 1993, Swengel and Swengel 1994, Swengel 1993b, 1995), presumably because the eggs that were present during the burns were killed by the fire. Only in one area with an incomplete burn were larvae recovered immediately after a fire (Swengel 1995). Maxwell and Givnish (1996) conducted larval surveys pre- and post-prescribed burning treatments and estimated 50 to 80% mortality on burned plots. The areas where larval feeding was observed in burn plots were at the bases of tree boles and downed logs where the fires skipped. The significance of these fire skips in the population biology of Karner blue remains to be determined. Adults can survive fire. Adults marked before a fire were recaptured after the fire at Necedah National Wildlife Refuge. Several fires were studied and the results indicate that Karner blue butterflies survived fire at rates ranging from 15 to 87 percent (King 1994). Adults presumably moved away from the site when it was burned to nearby adjacent habitat.

The effects of fire on Karner blue populations are not as clear as the effects of fire on individuals. The main complicating factor is the recolonization of burned areas from nearby populations. The rate of recovery after a burn has not been well characterized empirically. One hypothesis is that if colonization of the burned area by adults is slow or the population does not reproduce very fast, the detrimental effects of a burn could potentially last several generations. Conversely, if colonization is rapid and population growth high, then the effects of the burn could disappear rapidly. The available evidence supports these hypotheses.

In Wisconsin, Bleser (1993) and Swengel (1993a) reported findings from studies conducted at four sites in Wisconsin. Each site had areas that were burned and unburned. Estimates of Karner blue butterfly abundance were conducted using transect counts, one visit (sometimes more than one visit) to one transect per treatment area. This methodology provides general population trends following fire. Comparing the counts from the spring flights for 1991 (pre-burn) and 1992 (post-burn) suggests that abundance decreased at four of five burned sites (increase at one), but abundance also decreased at three out of four unburned sites (Swengel 1993a). Doing a similar pre- and post-burn comparison on the summer flight suggests that all sites (burned or unburned) decreased in abundance except for a small increase at one unburned site (Swengel 1993a). The variability in the data is too high to determine if the burned areas suffered a greater decrease than the unburned areas. The weather in 1992 was cool and wet, and sites throughout Wisconsin had low summer flight counts (Bleser 1993, Swengel 1993a), which suggests that annual variation in weather may have larger effects on populations than burning. At one site, Rynearson North in the Necedah National Wildlife Refuge, no adults were found following fire for either the spring or summer flights. Swengel (1995), however, reported that incomplete prescribed fires

with a return frequency of once every 3-4 years did not adversely affect Karner blue populations when a source population was nearby to recolonize the burned area. These data suggest that populations can be reduced or eliminated by fire, but it may also be possible that fire has only minor effects on Karner blue populations.

At Indiana Dunes National Lakeshore, selected areas were burned in fall, 1993 (Grundel 1994). Burned areas were adjacent to other areas with Karner blue populations. Compared to adjacent unburned areas, during 1994 first brood leaf feeding in the burned areas was reduced to six percent that of the unburned area, and second brood leaf feeding was still only 33 percent that of the unburned area. Thus, even when recolonization could be rapid, fire can reduce populations for at least one year post-fire. At Ft. McCoy, burns were conducted in 1993, and evaluated during 1994 and 1995 (Maxwell and Givnish 1994, 1995). The area was surrounded by sites occupied by Karner blue and the burns did not reduce tree or shrub canopy cover. In 1995, trees were removed to reduce cover. First brood larval damage was reduced between 50-80 percent and subsequent adult populations were reduced by about 30-35 percent in the burned areas. Lupine growth was stimulated by the burn, and second brood larval densities were 20-50 percent higher in the burned areas. Subsequent adult populations were similar in the burned and unburned areas. Thus, when recolonization is high, Karner blue populations can recover rapidly from fires. By 1995, populations of Karner blue were similar on burned and unburned sites (Maxwell and Givnish 1996).

In Minnesota, degraded habitat (where no adults or larvae had been observed previously) adjacent to occupied habitat was burned in the spring (Lane in prep.). In two burn plots fifty lupine stems were searched during the summer brood, and five and six larvae (per 50 stems) were found. These larvae probably were the offspring of emigrating female butterflies from the populated adjacent, unburned areas. The spring burn killed many lower tree branches and ground layer vegetation, and the resprouting lupine may have been more apparent or preferable than lupine in the unburned area.

Givnish et al. (1988) provide an historical perspective on the problem of burn frequency. They analyzed historical fire records associated with the Albany Pine Bush and suggested that fires returned once every 6 to 18 years, with once in 10 years a likely average. They recommended that prescribed fire be used at the average historical frequency, or once every 10 years.

Currently available quantitative data suggest that fire can reduce Karner blue populations to 10-50% of previous population densities during the year after the fire. The amount of reduction may depend on the the duration, intensity, and thoroughness of the fire. The effects of fire during the second generation and second year post-fire are not clearly known. The rate of recovery appears to be faster with higher rates of recolonization and population growth. In one case, populations recovered within 2 years post-fire, but longer recovery periods are possible. Until more definitive data are available, fire should not be used too frequently to manage lands with Karner blue (refer to Appendix G).

Removal and suppression of trees and shrubs. Tree and shrub removal and suppression, such as by girdling, herbicide-killing or brush-hogging, can be effective ways of reducing canopy cover. Tree harvesting operations remove canopy and disturb soil, which could have beneficial effects on lupine and Karner blue. The effects of girdling or killing trees with spot application of herbicides is likely to benefit lupine and Karner blue, but this needs to be documented. Some trees may resprout after herbicide application. Suppression of shrubs with herbicides or brush-hogging may have short-term benefits, but the shrubs could resprout vigorously, necessitating additional management. In general, many of the methods for removal and suppressing tree and shrub canopy may have a net positive effect on lupine and Karner blue, but these effects should be documented.

Associated Species. Remnant native Karner blue habitats are home to an impressive variety of additional rare and imperiled plants and animals. Healthy communities once associated with barrens and savanna habitats have declined dramatically because of habitat conversion, fragmentation and disruption of disturbance regimes. The unique ecological conditions created by the xeric, sandy soils, drought-like conditions, and frequent fire disturbances produced a suite of species that, because of their specialized adaptations, rarely occur outside of barrens and savanna habitats. Thus, while Karner blue butterfly is perhaps the most conspicuous member of this highly specialized community, many other regionally and globally rare species are also dependant upon these same habitats. Because barrens and savannas are rare habitats in many of the states with extant populations of Karner blues, many of the species restricted to these habitats are regionally imperiled. The ecologies of many of these species is not well enough understood to know how adapted these species are to other contemporary anthropogenic habitats. Appendix D lists the occurrence of Federal and state imperiled species known to be associated with savanna and barrens communities in those states with designated recovery units for the Karner blue. These lists were compiled by the State agencies responsible for rare species. Consequently, not all of the species listed will be found in occupied or occupiable Karner blue habitat, and not of the species that are rare in Karner blue habitat will be listed. These listings indicate that preserving and managing these dynamic barrens and savanna habitats is likely to have beneficial effects on ecological and biodiversity values (Table 4).

A bunchberry, *Cornus canadensis* in Indiana and Kirtland's warbler, *Dendroica kirtlandii* in Wisconsin are the only federally endangered species included in these lists. The following species are listed as federally threatened species: bald eagle, *Haliaeetus leucocephalus* in Michigan, and prairie bush clover, *Lespedeza leptostacnya* in Wisconsin.

In Wisconsin, Kirk (1996) conducted a thorough review of the rare species associated with dry prairie, barrens, and savanna in Wisconsin. Of the initial list of 122 species, 41 species were identified as associated with Karner blue habitat in the known range of the butterfly (1994 range). This list was further refined to those species that are highly associated with Karner blue habitat, and eight species were identified. All eight species are insects, including four butterflies, two skippers, and two tiger beetles. A ninth species, sharp-tailed grouse was identified of being of

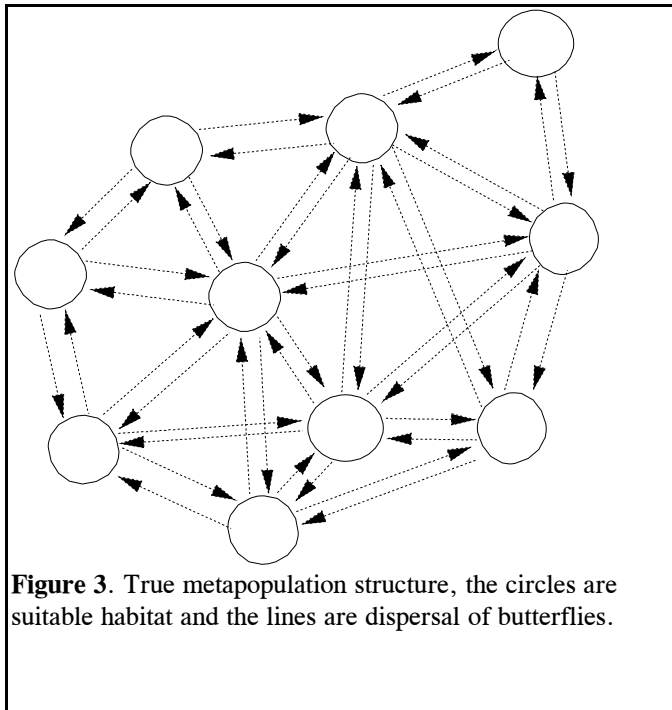
concern because of its large habitat needs.

Table 3. Number of designated State endangered, threatened, or special concern species potentially associated with with Karner blue habitats for each State with extant Karner blue populations. The number of species that are listed as Federal endangered, threatened, or species of concern is in parentheses. The number of invertebrates does not include Karner blue, and not all federally listed species are listed by each State.

State	Vertebrates	Invertebrates	Plants
New Hampshire	0 (0)	3 (0)	0 (0)
New York	0 (0)	0 (1)	3 (1)
Michigan	11 (3)	15 (3)	50 (4)
Indiana	8 (3)	2 (1)	24 (2)
Wisconsin	26 (5)	42 (5)	50 (5)
Minnesota	5 (1)	3 (0)	9 (0)

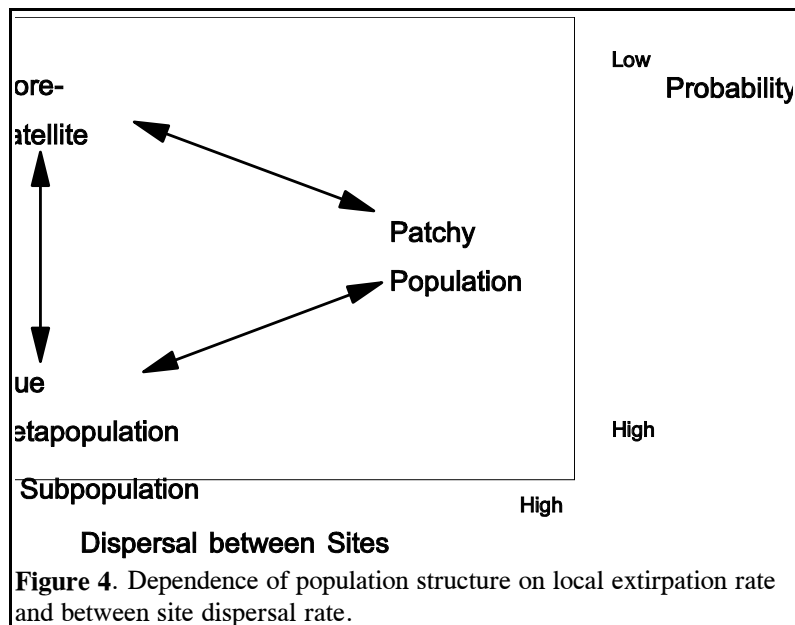
Population Structure

Spatial Structure of Karner Blue Butterfly Metapopulations. Karner blue butterfly populations have a metapopulation structure. For the purposes of recovery planning, a metapopulation is defined as a "population of populations." Such a metapopulation is distributed across a landscape at relatively discrete sites. Each of the relatively discrete sites that harbors Karner blue butterflies will be referred to as a subpopulation (these are sometimes referred to as local populations). In this definition of metapopulation there is no assumption about the relative importance of different subpopulations or about the significance or magnitude of dispersal between sites. Regardless, the number of subpopulations present at any given time is governed by the spatial structure of suitable and unsuitable habitat and the balance between local extirpation and local colonization.



Several theoretical spatial population structures are consistent with this definition of metapopulation. Levins (1969) described a population structure that will be referred to for recovery purposes as a true metapopulation (Figure 3). This assumes that all subpopulations are subject to extirpation, and that the probability of extirpation is identical but independent (asynchronous) among subpopulations (the thin white circles in Figure 3 designate that each site is subject to extirpation). Recolonization is slow and occurs at a rate that increases when there are more subpopulations (the dotted lines in Figure 3 indicate that dispersal rates are low). Persistence of a true metapopulation requires that colonization of suitable, unoccupied habitat occurs at a greater rate than subpopulation

extirpation. In a true metapopulation each subpopulation could contribute critically to metapopulation persistence. Therefore the destruction of even one subpopulation, or separation of subpopulations by dispersal barriers could result in the extinction of the entire metapopulation. This occurs only in the most precarious of true metapopulations, but this fact emphasizes that the persistence of a metapopulation is closely tied to both the spatial structure and persistence of all subpopulations and the rate of recolonization of all sites of suitable habitat. Management of true metapopulations must take into consideration all of these factors.

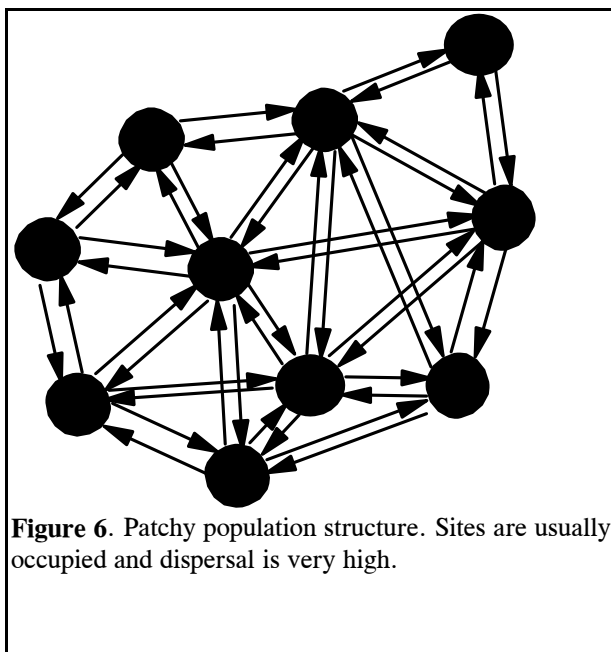
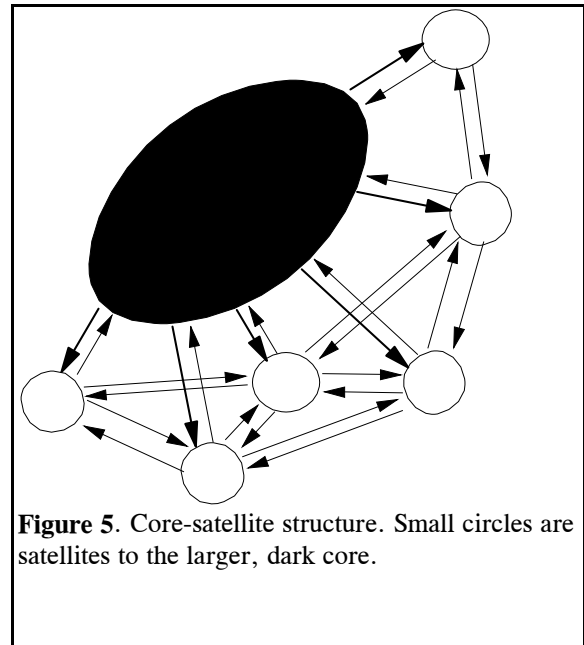


Another theoretical structure consistent with our definition of metapopulation is the core-satellite or mainland-island (Borman and Levitt 1973) structure (Figure 4). This structure differs from the true metapopulation structure by having at least one subpopulation that is immune to extirpation. This immune subpopulation is called the core; the core can have greater immunity to extirpation because of larger size, higher population numbers, better habitat, and so on (the shading in Figure 4 indicates that the core is

not extirpated). The bay checkerspot butterfly exhibits this type of metapopulation structure (Harrison et al. 1988). Individuals can disperse between the core and satellite populations, but the core is essential for the persistence of the metapopulation (the importance of dispersal from the core to the satellites is indicated by the thicker dispersal lines from the core to the satellite populations). If satellite populations are extirpated, they are eventually recolonized from the core, but if the core is extirpated, then the satellites will fail too. Management of core-satellite metapopulations must focus on the core.

A third theoretical structure that fits our definition of a metapopulation is the patchy population (Figure 5). A patchy population is distributed in discrete sites (or patches) on the landscape, but has dispersal rates that are so high that the subpopulations do not fluctuate independently (the high dispersal rates are indicated by the thick lines connecting sites). Colonization is so rapid that high populations in one subpopulation rapidly disperse to increase population densities in all subpopulations, and subpopulations rarely are extirpated (the rarity of extirpation is indicated by the shading of the sites in Figure 5). The subpopulations actually function as a single integrated deme (a randomly mating population) and all subpopulations fluctuate in more or less unison. In this case, the metapopulation only superficially has spatial structure because all subpopulations are interacting strongly.

Persistence of a patchy population depends on the size and stability of the whole metapopulation and not as much on the structure and relations among subpopulations. Management of a patchy metapopulation can focus on the average behavior of subpopulations across all occupied sites rather than focusing on a few to many critical sites.



In summary, a core-satellite structure implies that at least one site will never be extirpated (Probability of extirpation = 0), whereas in a true metapopulation all sites have equal probability of going extinct (Probability of extirpation = constant \neq 0). These idealized structures represent extremes along a continuum of extirpation probabilities (Figure 6). Both of these structures (true metapopulation and core-satellite) assume that site colonization rates are not extremely high for any site. The patchy population structure, in contrast, assumes that colonization rates are very high for all sites. Thus, the patchy population represents an extreme along a continuum of recolonization rates, with both the true metapopulation and core-satellite structures on one end, and the patchy

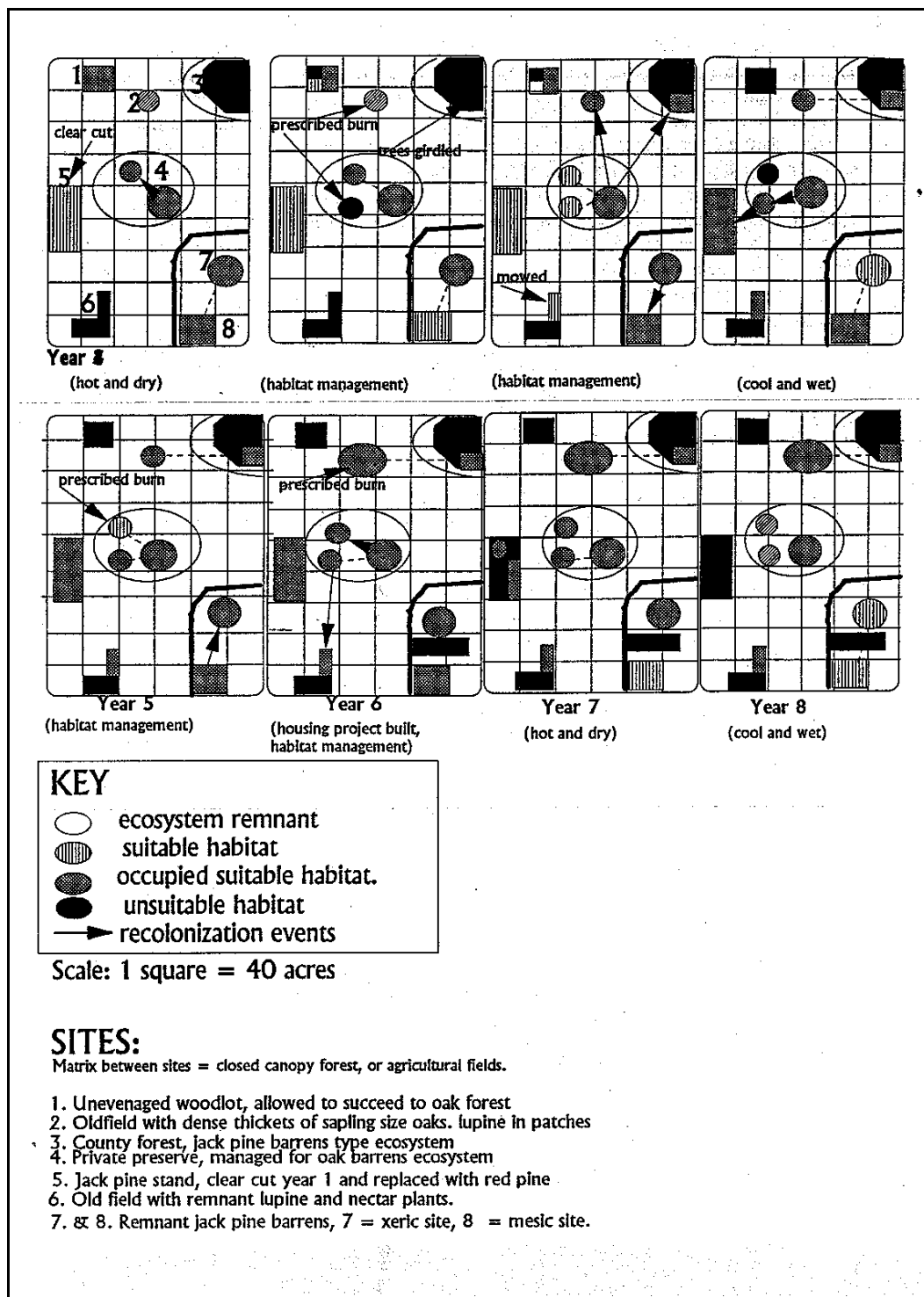
population structure on the other end of the continuum. Again, neither of these extremes are likely to be precisely accurate representations of an actual metapopulation of Karner blue butterfly. Management of a true metapopulation is likely to be more intensive than management of either a core-satellite or a patchy metapopulation, because of the need to keep track of each subpopulation individually in a true metapopulation. Consequently, one management strategy to reduce the cost of management is to use management to change the population structure to be more like a core-satellite or patchy metapopulation.

Together these theoretical structures probably encompass all likely structures of actual Karner blue populations, although none by itself may provide an accurate representation of any Karner blue metapopulation. Actual population structures of Karner blue butterfly are likely to be vastly more complex than any of these three common theoretical abstractions. For example, Karner blue metapopulations are unlikely to have a core-satellite structure because all sites are involved in successional processes that eliminate Karner blue followed by renewal events that rejuvenate habitat; a single site is unlikely to maintain a healthy, stable subpopulation of Karner blue butterflies indefinitely (Givnish et al. 1988). Management efforts can be used to reduce the probability of extirpation of a site, but it may be difficult to manage a single site so that it persists indefinitely into the future. It is also unlikely that Karner blue metapopulations have a true metapopulation structure. All sites will not have a uniformly high probability of extirpation, with some sites being more prone to extirpation than others, and the probability of extirpation among sites is probably correlated in time and space. Protection from extirpation probably exists at many sites that provide refugia from various types of disturbance but not others. For example, mesic areas would be temporary refugia from drought or fire, whereas xeric areas would be temporary refugia from the threats of cold weather and canopy closure. Consequently, the probability of extirpation is unlikely to be constant or independent across sites or at a single site over time. It is unlikely that Karner blue metapopulations are patchy metapopulations. This structure requires high rates of recolonization that integrate the local population dynamics of the spatially distributed metapopulation. Some metapopulations may appear to function as patchy populations because they occupy many sites and the sites are close together, however dispersal must be very high to integrate the population dynamics across the entire metapopulation. Even at the Necedah National Wildlife Refuge in Wisconsin, where dispersal rates are the highest measured for Karner blue (King 1996), subpopulations do not fluctuate together (King 1994).

Figure 7 presents a hypothetical example to illustrate some of the complexity of the functioning of an actual metapopulation, showing how subpopulations might interact, suitable habitat colonized, and occupied sites extirpated. In this example, three local populations are within a remnant of healthy barrens or savanna ecosystem (center oval), and other sites are associated with private and county forest lands or poor quality remnant barrens or savanna ecosystems. The sites are renewed by various disturbances or efforts to restore barrens/ savanna ecosystems. The sites decline in suitability for Karner blue according to plan or because of lack of management. In this example, the small group of subpopulations associated with the remnant healthy barrens or savanna ecosystem together function as a core group of subpopulations. Together they are managed so that one or more of them harbors a strong subpopulation of Karner blue butterfly,

and when considered together, Karner blue butterfly may persist indefinitely on them. This kind of metapopulation structure, with a core group of subpopulations, is intermediate to all of the theoretical abstractions described above, but preserves many of the management advantages of the core-satellite structure.

Figure 7. Schematic representation of a functioning metapopulation



The broad metapopulation concept used in this recovery plan enables a robust description of a viable metapopulation, because it focuses on the factors that create a healthy metapopulation, including sufficient suitable habitat to support a metapopulation, sufficient connectivity to promote recolonization, and management guidelines to aid decision-making. Because Karner blue metapopulations are likely to exhibit considerable variation in spatial structure, the concept of viable metapopulation must be applicable to all possible spatial structures, including the many variants of true metapopulations, core-satellite metapopulations, and patchy metapopulations.

A viable metapopulation of Karner blue butterfly must be large enough, have a sufficient geographic base, and managed and monitored to persist indefinitely over time. The management and monitoring system must buffer the metapopulation against adverse disturbances and threats to survival, maintain suitable habitat over time in an appropriate spatial structure, and identify appropriate responses to potential declines in the metapopulation. This definition of viable metapopulation is elaborated in Appendices E and F. It should be clear that the definition of a viable population does not depend on assuming that all metapopulations of Karner blue are true metapopulations. If a Karner blue metapopulation is in fact a true metapopulation, however, the definition of viable metapopulation should indicate what would be needed for this true metapopulation to be a viable one. Moreover, the definition of viable metapopulation does not encourage a minimalistic perspective; if the metapopulation can be made more secure, the management and monitoring costs can decrease.

Management is a crucial component of a viable metapopulation, and because complete information is not available, adaptive management for improving or maintaining Karner blue metapopulations is essential. Several adaptive strategies can be pursued. Management can be adapted to change the structure the metapopulation. In today's managed landscapes, we may impose a spatio-temporal structure on a metapopulation to create or maintain a metapopulation more like a core-satellite or patchy structure. These kinds of metapopulations may be more robust to disturbances and threats and will probably be less expensive to maintain. The geographic base of the metapopulation also can be managed adaptively over time. New areas can be added and old areas eliminated from the metapopulation as information about its functioning improves. Monitoring can be adapted as the duration of successful management increases. As confidence is gained in the management practices, the need for monitoring declines.

Metapopulation Persistence. Persistence of a Karner blue metapopulation will be governed by the balance between extirpation of subpopulations and recolonization of unoccupied sites of suitable habitat. Recolonization rates will be related to colonization rates and between site dispersal rates, and as these increase, occupancy of suitable habitat will increase and the metapopulation may become more integrated, functioning like a patchy metapopulation. Subpopulation extirpation rates will be related to the extent and quality of habitat and the rate that habitat degrades from factors such as canopy closure. If management activities operate to reduce the rate of extirpation for one or a cluster of subpopulations, the metapopulation becomes stabilized around the dynamics of that subpopulation(s), functioning more like a core-satellite

metapopulation. Both of the rate of recolonization and the rate of extirpation can be influenced by spatial structure of the habitat mosaic.

Recolonization. Recolonization rates will be affected by the rate and pattern of dispersal, and the availability of suitable habitat for colonization. Most adults move short distances (less than 200 meters or 219 yards), and a small percent move more than one kilometer (0.62 miles). The limited data suggest that the closer the sites and more open the intervening habitat, the more observed between-habitat movements. Therefore recolonization rates are expected to be higher when there is a large number of suitable habitat sites per unit area, which reduces inter-site distance. In addition, dispersal may be facilitated by corridors of open habitat. Refer to Appendix G for suggestions that may help increase recolonization rates.

Extirpation. Savignano (1994b) demonstrated that extirpation of subpopulations does occur. She found that in Saratoga County, NY, only 52 percent of sites that had been recorded previously with Karner blue were still occupied in 1990. Informal observations by numerous researchers have confirmed that subpopulations of Karner blue become extirpated, but the reasons for extirpation remain poorly understood.

The probability of extirpation of a subpopulation may be affected most by the extent and quality of suitable habitat, and secondarily by chance events. Clearly, a healthy, abundant lupine population is essential for continued persistence of a subpopulation. Savignano (1994b) showed that subpopulations on sites with more lupine are more likely to persist than those on sites with less lupine. Microhabitat diversity (as created by variation in canopy cover and possibly by variation in topography, aspect, and soil hydrology) probably should reduce the probability of extirpation, because immature survival is higher in shady microhabitats, by protecting against year-to-year environmental variation. The importance of nectar plants for persistence is less well documented. Lack of nectar plants appears to increase adult mortality rates (Clench 1967, Watt 1979), and it is expected that a diversity of nectar plants would improve persistence. Different nectar plant species are differentially affected by variation in weather. For example, during the 1995 drought at Waupaca, WI, most of the lead plant (*Amorpha canescens*) flowers aborted, while hoary allysum (*Berteroa incana*) and horsemint (*Monarda punctata*) still flowered (Lane, personal communication). Similarly, in NY the phenology of *Ceanothus americanus*, a major second brood nectar source, matches Karner blue phenology poorly in some years and quite well in others (Schweitzer, personal communication).

It is widely believed that uninterrupted, succession will cause extirpation (Givnish et al. 1988, Helmbolt and Amaral 1994, Sommers and Nye 1994, Grigore and Windus 1994, Packer 1994). Lupine is eliminated when tree canopy closure occurs (Celebrezze 1995), but the timing of extirpation of subpopulations of Karner blues is poorly understood (how much before or how much after canopy closure). Moreover, the rate of canopy closure is quite variable from site to site and heterogeneous within sites, so the overall importance of succession as a cause of extirpation is may vary from location to location. Finally, management, or the lack thereof, can influence the rate of canopy closure. Indeed, the lack of management has allowed succession to

proceed unimpeded in many habitats, which may have resulted in reduced lupine and reduced Karner blue populations (Givnish et al. 1988, Helmbolt and Amaral 1994, Sommers and Nye 1994, Grigore and Windus 1994, Packer 1994).

Larger areas of suitable habitat will tend to produce more butterflies, which will tend to protect the subpopulation from extirpation. Conversely, very low population numbers may be associated with an increased probability of extirpation because of chance environmental, demographic, and genetic events. Random environmental events can push already small subpopulations to extirpation. This may occur for example if a fragmented and sparsely populated subpopulation is burned by a wildfire. The remaining pockets of individuals and habitat may be so small that inability to find mates, inadequate lupine or nectar plant resources, or inbreeding depression may push the subpopulation to extirpation (see Lawrence 1994). Recurrent drought may have been involved in the extirpation of the Ontario populations (Packer 1994, Schweitzer 1994a). It is also thought that very small subpopulations are more susceptible to extirpation from demographic stochasticity (skewed sex ratio, chance birth or death rates) (Schonwald-Cox et al. 1983). For example, a widespread, but patchily-distributed European lycaenid *Plebejus argus* L. has higher extirpation rates in small areas of suitable habitat than large ones (Thomas and Harrison 1992).

Spatial structure of habitat mosaic. Many environmental effects that are potentially detrimental to Karner blue can extend over extensive areas, such as large-scale wildfire, extended periods of extraordinary weather (summer-long, hot droughts or extremely delayed and cool summers) or disease epidemics. In these cases, local extirpation is likely to increase throughout the metapopulation, perhaps to the point that the entire metapopulation has no chance of recovery. The importance of these factors on metapopulation persistence has been inadequately investigated, but year-to-year variation in weather may be responsible for some of the large fluctuations in butterfly abundance that have been observed in Wisconsin (Bleser 1993, Lane 1996).

Variation in patch size and quality between local populations should increase persistence of a true metapopulation by producing asynchronous fluctuations in the density of subpopulations. A core-satellite structure might be stabilized against these large-scale disturbances by managing the metapopulation to have more than one core subpopulation or clusters of subpopulations. A patchy population might be stabilized by being spread over a large spatial area.

Threats to Survival

The most important threats to Karner blue rangewide are habitat loss, which has been accompanied by increased fragmentation of the remaining suitable habitat, and habitat degradation, primarily caused by ecological succession. Related to these is the threat of inappropriate management stemming from conflicting and potentially conflicting management objectives. Large-scale disturbances, such as large wildfire and unusual weather, also present a real threat to Karner blue populations. Other factors may pose real threats in particular instances, but for the most part these other factors have not been adequately investigated. Detailed discussion of the threats to Karner blue in each recovery unit is provided in Appendix B.

Habitat Loss, Alteration, and Destruction. The loss and degradation of Karner blue butterfly habitat detrimentally affects its population several ways. Habitat loss has resulted in fewer subpopulations, greater distances between suitable habitat sites, and smaller sites. Habitat degradation has reduced microhabitat diversity, and the abundance and quality of food resource (lupine and nectar plants). New sites with suitable habitat are created infrequently without appropriate management, and areas in between subpopulations may degrade, reducing the colonization rate. Less direct effects could also occur. For example, if disturbance processes are inhibited, then the remaining habitat may become restricted to steep open sand banks. During drought years, lupine may senesce early, decimating the subpopulation and reducing the probability that the metapopulation will persist.

Loss of native habitat. The major threat to native habitats is conversion to alternate uses, such as agriculture, silviculture, industrial, residential and commercial development, and road construction. Originally, barrens and savanna were widespread in central United States but rare in eastern United States. In both regions there has been a precipitous decline in these habitats. Remaining barrens and savanna usually consist of isolated patches which persist because of droughty soils, insects and disease, and human disturbance such as mowing, light grazing and intermittent prescribed fires. This translates into a significant loss of suitable habitat for the Karner blue butterfly and habitat loss continues to threaten butterfly populations across its range.

Degradation of native habitat. The major threats to survival of Karner blue butterfly in native habitats are, succession to woodlands and forests, and management for other wildlife and natural areas goals that do not take into account the needs of Karner blue butterfly, such as restoration and maintenance of native vegetation, encouragement of game animals, and recreational use. Human use of these native habitats and adjacent developed habitats has often resulted in suppression of disturbance and decline of Karner blue butterfly populations. Although in many cases, wildlife and other management goals are concordant with enhancement of Karner blue, in many cases too vigorous a pursuit of these other goals can be detrimental to the butterfly.

Loss of non-native habitat. Karner blue butterfly inhabits several non-native habitats, including some silvicultural habitats, mowed rights-of-way, and roadside verges. These habitats are being lost to more intensive development pressures. Silvicultural habitats that are suitable for Karner

blue are being converted to more intensive silvicultural uses that are less compatible and to incompatible residential and commercial uses. Along roadsides, native vegetation is being replaced by a more uniform, exotic vegetation. It is hypothesized that conversion of former jack pine plantations to red pine results in a loss of Karner blue habitat because red pine canopy is thicker and closes more rapidly, but this requires confirmation.

Degradation of non-native habitat. Silvicultural habitats degrade as suitable Karner blue habitat as the crop matures and canopy closure occurs. This is natural part of the production cycle, and as long as other silvicultural habitat is opened up, such as by harvesting, the metapopulation can remain at viable levels. These silvicultural habitats can be degraded for Karner blue in other more subtle ways, such as by changing the management objective for land that was previously suitable for the butterfly. Shifting objectives can change the balance between the duration of a Karner blue subpopulation on a site and the proportion of total area that is suitable for the butterfly. For example, suppose a particular silvicultural objective results in canopy closure occurring by 10 years after planting and maturation and harvest in year 40. If a Karner blue subpopulation uses a site for 8 of the 10 years before canopy closure, then 20 percent of the land managed for that objective could have habitat suitable for Karner blue butterfly. If the land is managed for a different objective, so that canopy closure occurs faster and subpopulations can only persist for 6 years, and stand maturation takes 60 years, then only 10 percent of the land managed for this objective could have habitat suitable for Karner blue. The exact percentage will vary from year to year depending on the proportion of the land harvested, variation in growth among sites, and changes in management objectives for a particular site. The longer the subpopulation can persist at higher population numbers, in general, the better for Karner blue butterfly.

Karner blue butterfly also inhabits power line and railroad rights-of-way. If these are managed with herbicides or mowing from the late spring to the early summer, they would suppress lupine and nectar plants, thereby becoming poor habitat for Karner blue butterfly.

Types of inappropriate management. Inappropriate management practices threaten some populations of Karner blues. These inappropriate practices occur because land managers have several management goals and they either are unaware how pursuit of these other goals could have detrimental effects on Karner blue butterflies or they judge the trade-off with its detrimental effect on the butterflies to be acceptable. Several examples of inappropriate management practices are described in what follows.

(1) Pest control. Poorly timed or poorly located use of herbicides can have a negative effect on Karner blue butterflies, by killing or suppressing lupine or important nectar plants. The direct effect of herbicides on Karner blue larvae is under investigation. Most insecticides are not target-specific and can kill most insects in the treated area. In laboratory tests, even the relatively specific insecticide, *Bacillus thuringiensis kurstaki* (BT), kills all larval instars of Karner blue (Herms 1996). Because the timing of insecticide applications for gypsy moth control typically

coincides with the larval stage of the Karner blue, inappropriate application of insecticides could adversely affect Karner blue (Herms 1996). Miller (1990) found that BT reduced the number of non-target Lepidoptera species and suggested that if any of the species had been limited in its distribution, it would have been at high risk of becoming extirpated. The effect of biological control agents on non-target insects is poorly documented. Analysis of the effects of releases of the biological control agent *Trichogramma nubilale* (Andow et al. 1995) showed the risk to be small. An examination of the introduced insect predator *Coccinella septempunctata* in Karner blue habitat (Schellhorn et al. personal communication) suggests that the risk could vary with predator density, prey density, and microhabitat. The direct or indirect effects of fungicide applications on Karner blue butterfly is not known.

(2) Mowing. Mowing between late spring and early summer may have detrimental effects on Karner blue populations. Mowing can damage lupine, eliminating food for larvae. Although it may reduce shade and competition, mowing may favor plant species not used by Karner blue butterflies (Givnish et al. 1988). Mowing during adult nectaring periods can greatly reduce flower number and nectar availability. In addition, mowing can kill larvae that are present during mowing. Mowing of lupine before seeds mature and disperse could reduce reproduction by lupine, and have a long-term detrimental effect on Karner blues.

(3) Prescribed fire. One of the most useful restoration and management tools, prescribed fire, may threaten Karner blue populations if the burning is conducted on the majority of the habitat, and if high intensity fires are used at frequent intervals. Annually conducted prescribed fires will improve barrens and savanna vegetation (Tester 1989), but these would likely be detrimental to Karner blue butterfly.

(4) Deer and grouse management. High deer densities can devastate Karner blue butterfly habitat and cause direct mortality by ingestion of larvae (Packer 1994, Schweitzer 1994). Schweitzer recommends that deer populations be managed to levels where no more than 15 percent of lupine flowers are consumed (Schweitzer 1994), but this recommendation has not been rigorously tested. Grouse habitat does not support lupine, because the dense, shrub vegetation favored by these game birds casts too much shade to allow lupine to thrive.

Overutilization for Commercial, Recreational, Scientific, or Educational Purposes. In the past the Karner blue butterfly has been collected (USFW 1992), and this has not been considered a significant factor in population decline. In the parts of its range where only a few small populations remain, however, extensive collections could have a detrimental effect. Although it has been suggested that collecting of Karner blue butterflies in Illinois in the

Kenosha Potential Recovery Unit may have contributed to the recent extirpation of the butterfly in this Unit, only three butterflies were collected and it is highly unlikely that this could have contributed to the extirpation.

Disease or Predation. Very little research has been conducted on the natural enemies of Karner blue butterfly, so the significance of these biotic factors as threats to Karner blue cannot be stated. Similar to most other insects, mortality of immature life stages is very high (Savignano 1990, Lane 1994b). Part of this mortality is caused by predators, parasitoids, or pathogens (Savignano 1990). Larval predators include pentatomid stink bugs (*Podisus maculiventris*), wasps (*Polistes fuscatus* and *P. metricus*), ants (*Formica schaufussi* and *F. incerta*) (Savignano 1990, 1994a), spiders (Packer 1987), and ladybird beetles (*Coccinella septempunctata*) (Schellhorn et al. personal communication). Four larval parasitoids were reared from field collected larvae: a tachinid fly (*Aplomya theclarum*), a braconid wasp (*Apanteles* sp.), and two ichneumonid wasps (*Neotypus nobilitator nobilitator* and *Paranoia geniculate*) (Savignano 1990). Several insect predators have been observed attacking adults including: spiders, robber flies, ambush bugs, assassin bugs, and dragonflies (Bleser 1993, Packer 1987). Disease pathogens of Karner blue butterfly have not been identified, but probably exist.

It is unknown whether birds or mammals cause significant mortality at any life stage of the Karner blue butterfly. Bird beak-marks are occasionally observed on adult wings. Heavy browse by mammals or insect herbivores on lupine in Karner areas can also have a detrimental effect. Effects will be most dramatic if larvae are ingested when lupine is consumed, or if they starve because lupine is severely defoliated. Browse or herbivory on the flowers or fruits can reduce lupine seed and possibly affect the long term survival of the lupine population (Straub 1994). Insect herbivores, such as painted lady larvae (*Vanessa cardui*) and blister beetles, can defoliate high percentages of the lupine in an area, which may result in larval starvation.

Aggressive plant species may pose a threat by out-competing other plant species required by the Karner blue butterfly. Orange hawkweed (*Hieracium aurantiacum*) and Pennsylvania sedge (*Carex pennsylvanicus*) can dominate some Karner blue habitats and reduce lupine and the diversity and abundance of nectar plants available to the Karner blue adults. Spotted knapweed (*Centaurea maculosa*) is used as a nectar plant, but its dominance can reduce the diversity of nectar plants, increasing the risk of extirpation of the subpopulation. In the absence of management, dense cover of buckthorn (*Rhamnus catharticus*), American hazelnut (*Corylus americana*), or other woody shrubs will eventually eliminate lupine.

Plant diseases of lupine could reduce its food quality or rendering it unsuitable, resulting in larvae mortality or reduced adult fecundity. Lupine leaves are attacked by both powdery mildew (*Erysiphe polygoni*) and a leaf rust (*Puccinia andropogonis*). No research has been conducted to determine whether these diseases result in reduced lupine quality.

Of particular interest is how fragmentation and degradation of habitat influences the population dynamics of natural enemies and competitors of Karner blue butterfly and lupine, and the ultimate effect on Karner blue metapopulations. For example, the abundance of predators and parasitoids varies with tree canopy cover and therefore some microhabitats may provide refugia for Karner blue (Lane 1994b, Schellhorn et al. personal communication).

Inadequate Regulatory Mechanism. Karner blue butterfly is listed as a state endangered species in Minnesota, New York, New Hampshire, Indiana, and Ohio. In Michigan it is listed as threatened, and in Wisconsin it is listed as a species of special concern. It is not listed in Illinois because it has been extirpated from the state.

While most states still supporting butterfly populations have legislation that protects the butterfly, provisions for protection and management of the habitat are incomplete to non-existent (USFW 1992). This is an important gap in that loss and degradation of suitable habitat are primary reasons for population extirpation and decline in numbers, and recovery of the species will depend on ensuring an adequate base of suitable habitat. Implementation of management agreements, development of conservation easements, and outright land purchase could be used to ensure the habitat base. Other, more flexible regulatory mechanisms could be developed to ensure this habitat base.

Populations of Karner blue that occur on Federal and State lands are protected from destruction, but Federal and State land managers might not manage actively for appropriate savanna or barrens habitat. Developing stream-lined procedures for incorporating concerns for Karner blue butterflies into current management plans would be useful.

Other Natural or Man-made Factors Affecting Its Continued Existence. Unusual weather can negatively affect Karner blue populations. Spring and summer drought can stress lupine and may reduce larval populations, and reduce flowering of nectar plants (Lane, personal communication), which may result in greater adult mortality. Cool springs can delay lupine emergence until after Karner blue egg hatch (Lane, personal communication). Cold, wet weather during the flight periods reduces the time available for oviposition and could increase adult mortality. A combination of drought and cool, wet springs is one of the suspected causes of population extirpation in Ontario (Packer 1994, Schweitzer 1994a).

Large-scale wildfire could destroy a large metapopulation. These events are infrequent, but are devastating nonetheless. Although these rare events would have large detrimental effects for several years, it is possible that the metapopulation could recover if enough healthy unburned populations existed nearby.

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